Predator-prey Interactions in a Human-dominated Landscape

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Contents

Summary		1
Zusammenfassung		3
General Introduction		5
Chapter 1	Spatial scale and behavioral state interact in shaping temporal dynamics of habitat selection in Eurasian lynx	22
Chapter 2	Caught in the crossfire of two predators – Hunting-mediated predator facilitation results in superadditive mortality of European roe deer by Eurasian lynx	61
Chapter 3	Strong non-consumptive effects of a large vertebrate ambush predator reduce the survival of one of its main prey	98
General Discussion		125
Author contributions		132
Addresses of co-authors		133
Curriculum vitae		134
Acknowledgments		135

Summary

Understanding animal space us is a fundamental concern in Ecology. Predator-prey interactions are a behavioral response game where predators try to find prey, and prey are trying to avoid the predators, thereby shaping animal space use and habitat selection. In the process both predator and prey tradeoff between risk avoidance and food acquisition in order to maximize their fitness. As such predator-prey dynamics have fascinated many generations of ecologists.

At the same time the impact of human activities on ecosystem processes have become increasingly evident over the years and almost all habitats on earth today have been altered to some degree by humans. As a consequence humans can be considered as ecological players of ecosystem processes that shape the behavior and demography of their commensal species. In the presence of humans large top predators may be downgraded in the food chain or compete with humans for their prey. Furthermore prey species themselves have to tradeoff between risk avoidance towards humans or their natural predators.

It was the goal of this thesis to look at various aspects involved in shaping the space use patterns of the Eurasian lynx (Lynx lynx) and its main prey, the European roe deer (Capreolus capreolus) and to characterize the spatiotemporal drivers of habitat selection and risk avoidance of both players in a human dominated environment. By focusing on both predators and prey I identify different key components of the behavioral response game between Eurasian lynx and European roe deer.

In the first chapter I investigated how tradeoffs between risk avoidance and resource abundance in human-altered environments affect habitat selection of Eurasian lynx. In particular, I studied how spatial scale interacts with the intrinsic behavioral state of Eurasian lynx in shaping the response to temporal and spatial fluctuations in human activity and prey availability. I show that lynx tradeoff between anthropogenic risk and prey density by using areas of high prey density during times of low human disturbance. This tradeoff differs among behavioral states and is dependent on the spatial scale considered.

In the second chapter I focused on the prey and tested how lynx and humans interact in shaping space use patterns of roe deer during the hunting season in fall. Multiple predators of a single prey may positively or negatively interact with each other via their prey. The same may be true for human hunters that compete with natural predators for the same prey. I explored how roe deer tradeoff between hunting and lynx predation risk and whether hunting increases the deer's susceptibility to lynx predation. I found that roe deer avoid areas of high hunting risk during the hunting season at the expense of higher exposure to lynx predation risk. Furthermore there was strong evidence that lynx increased their hunting effort and hunting success during this time period. The results provided strong evidence that hunters facilitated lynx predation which resulted in superadditive mortality for deer during the hunting season.

In environments with limited resources and time antipredator behavior may come at costs that ultimately affect prey demography. The strength of such non-consumptive effects (NCE) largely depends on the hunting mode of the predator. Ambush predators exert stronger NCE than active predators as they provide more persistent cues about predation risk than their widely roaming counterparts. While evidence comes from different taxonomic groups, evidence from large mammalian predator-prey systems is rare and equivocal. In the third chapter I looked at the occurrence and strength of NCE of the ambush predator, the Eurasian lynx on its main prey the European roe deer. According to ecological prediction I found that lynx evoked strong NCE that increased non-lynx-related mortality of roe deer in the study area.

In summary, I focused in this thesis on identifying key drivers involved in shaping space use patterns of a large ambush predator and one of its main prey. Furthermore I characterized the spatiotemporal drivers of food acquisition and risk avoidance of both players in a human dominated environment. The presented results illustrate the tradeoffs between risk avoidance and food acquisition that affect decision making of all animals and show the potential costs of these tradeoffs in the form of reduced survival or reproduction. Finally the findings highlight the role of humans as ecological drivers of Ecosystem processes and may help developing efficient wildlife management plans that are needed for the conservation of large predators and their prey alike in human altered environements.

Zusammenfassung

Es ist ein grundlegendes Anliegen in der Ökologie die Raumnutzung von Tieren zu verstehen. Räuber-Beute Interaktionen widerspiegeln ein Versteckspiel bei welchem der Räuber versucht die Beute zu finden, während dem die Beutetiere versuchen dem Räuber auszuweichen. Diese gegenseitige Beeinflussung zwischen Räuber und Beute bestimmt zu wesentlichen Teilen die Raumnutzung von Tieren, bei welcher sowohl Räuber als auch Beute zwischen Nahrungssuche und Risikovermeidung abwägen müssen mit dem Ziel die individuelle Fitness zu maximieren. Solche Räuber-Beute Beziehungen faszinieren Ökologen seit Generationen.

Gleichzeitig wurde der wachsende Einfluss von menschlichen Aktivitäten auf grundlegende ökologische Prozesse in den letzten Jahren immer deutlicher. Heutzutage sind fast alle Lebensräume zu einem gewissen Grade durch Menschen beeinflusst. In diesem Sinne können Menschen als ökologische Mitspieler betrachtet werden welche auf Ökosystem-Prozesse einwirken und dadurch das Verhalten und das Populationswachstum von anderen Arten beeinflussen können. In Anwesenheit von Menschen werden Top-Prädatoren in der Nahrungskette heruntergestuft oder sie konkurrenzieren mit Menschen um ihre Beutetiere. Zudem müssen Beutetiere selbst auch zwischen Menschenvermeidung und Prädatorvermeidung abwägen.

Es war das Ziel dieser Dissertation verschiedene Aspekte der Raumnutztung des Eurasischen Luchses (Lynx lynx) und seiner Hauptbeute, dem Europäischen Reh (Capreolus capreouls) genauer zu betrachten und dabei die räumlich-zeitlichen Faktoren, welche die Nahrungssuche und Risikovermeidung beeinflussen zu charakterisieren. Dadurch, dass ich sowohl Räuber als auch Beute untersuchte, konnte ich die Hauptkomponenten identifizieren, welche das Versteckspiel zwischen Luchs und Reh bestimmen.

Im ersten Kapitel untersuchte ich, wie die Abwägungen zwischen Risikovermeidung und Nahrungssuche in einer menschlich-geprägten Umwelt die Habitatsnutzung des Eurasischen Luchses beeinflussen. Insbesondere untersuchte ich wie die räumliche Skala und der momentane Verhaltenszustand zusammen die Reaktion eines Luchses auf räumliche und zeitliche Fluktuationen der menschlichen Aktivität einerseits und der Beuteverfügbarkeit andererseits beeinflussen. Ich kann zeigen, dass Luchse zwischen anthropogenen Risiken und Beuteverfügbarkeit abwägen, indem sie Orte hoher Beutedichte zu Zeiten niedriger menschlicher Aktivität nutzen. Diese Abwägungen wiederum werden beeinflusst durch den momentanen Verhaltenszustand und unterscheiden sich je nach der betrachteten räumlichen Skala.

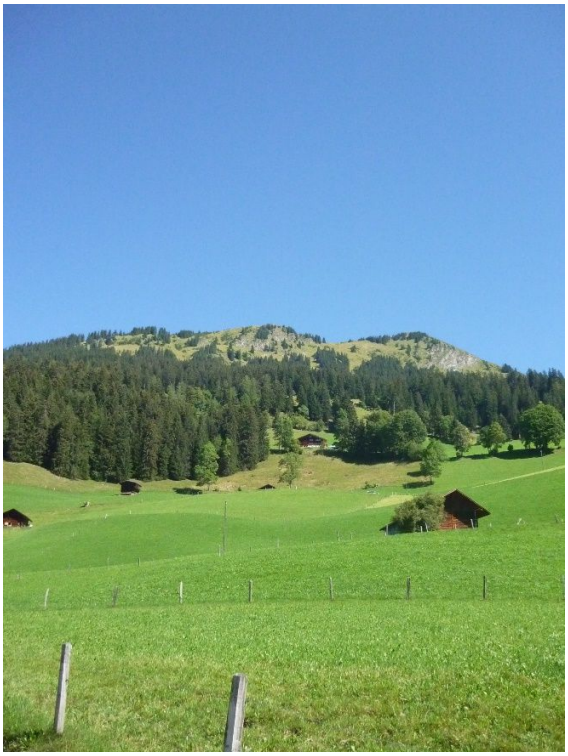
Im zweiten Kapitel stand das Beutetier im Vordergrund, wobei ich untersuchte wie Luchs und Mensch zusammen die Raumnutzung von Rehen während der Jagdsaison mi Herbst beeinflussen. Verschiedene Prädatoren derselben Beute können positiv oder negativ miteinander über dieselbe Beute interagieren. Das mag auch auf Jäger zutreffen, welche mit den natürlichen Prädatoren um dieselbe Beute konkurrenzieren. Ich untersuchte wie Rehe zwischen Jagdrisiko

und dem Luchs Prädationsrisiko abwägen und ob die Rehe während der Jagdzeit anfälliger sind von einem Luchs gerissen zu werden als ausserhalb der Jagdzeit. Die Resultate zeigen, dass Rehe Orte hohen Jagdrisikos vermeiden und dadurch vermehrt dem Prädationsrisiko des Luchses ausgesetzt sind. Des Weiteren fand ich starke Hinweise dafür, dass Luchse während der Jagdsaison ihre Jagdaktivität sowie ihren Jagderfolg steigern können. Diese Resultate zeigen, dass Jäger den Jagderfolg des Luchses positiv beeinflussen was superadditive Mortalität während der Jagdsaison zur Folge hat.

In einer Umwelt, in welcher Resourcen und Zeit limiterend sind, kann Antiprädationsverhalten mit Kosten verbunden sein, welche im Endeffekt das Populationswachstum von Beutetieren beeinflussen kann. Das Ausmass solcher indirekten Effekte für die Beutepopulationen hängt weitgehend vom Jagdmodus des Prädators ab. Dabei verursachen Anschleichjäger die stärkeren Effekte als aktiv jagende Prädatoren, weil erstere länger anhaltende Hinweise bezüglich Prädationsrisiko liefern als dies ihre aktiv jagenden Gegenspieler tun. Während dem dies für verschiedenste taxonomische Gruppen gezeigt werden konnte, fehlen für Räuber-Beute System von grossen Säugetieren die Hinweise weitgehend. Im dritten Kapitel untersuchte ich das Vorhandensein und Ausmass von indirekten Prädationseffekten des Luchses, ein Anschleichjäger, auf seine Hauptbeute, das Reh. Gemäss den ökologischen Vorhersagen konnte ich zeigen, dass Luchse starke indirekte Prädationseffekte bei Rehen hervorrufen, welche das Überleben von Rehen im Studiengebiet negativ beeinflussen.

Zusammenfassend, habe ich mich in dieser Dissertation darauf fokussiert die Hauptfaktoren zu identifizieren, welche die Raumnutzung eines grossen Anschleichjägers und seiner Hauptbeute bestimmen. Des Weiteren habe ich die räumlich-zeitlichen Einflussfaktoren, welche die Nahrungssuche und Risikovermeidung von Räuber und Beute in einer anthropogen geprägten Umwelt beeinflussen charakterisiert. Die hier präsentierten Resultate illustrieren die Abwägungen zwischen Risikovermeidung und Nahrungssuche, welche die Entscheidungsfindung von allen Tieren beeinflussen und zeigen gleichzeitig die potentiellen Kosten dieser Abwägungen in Form reduzierten Überlebens oder Reproduktion. Am Ende unterstreichen die Ergebnisse die Rolle des Menschen als ökologischer Faktor in Ökosystemprozessen und können dazu beitragen effiziente Wildtier-Management Pläne zu erarbeiten, welche für den Schutz von Grossraubtieren und ihren Beutetieren gleichermassen von Bedeutung sind.

General Introduction



Predator-prey relationships shape the space use patterns and habitat selection of animals in the wild and are therefore key drivers of ecosystem dynamics. All animals are exposed to risks in one way or another and most species are both predator and prey at some stage in their lives (Lima&Dill 1990). As a consequence individuals have to tradeoff between food acquisition and risk avoidance when moving through space in order to maximize their fitness. Understanding the way how predators and prey respond to each other and adjust their space use and behavior accordingly are prerequisites to explain predator-prey interactions in ecological communities and how these interactions propagate though the various trophic levels of an ecosystem.

Predator-prey interactions – a behavioral response game

Predators not only affect their prey by killing them but also by evoking behavioral responses in the form of antipredator strategies (Lima&Dill 1990). A fundamental assumption underlying ecological theory about the behavioral response of prey to predators is the ability of prey to perceive the level of risk they are exposed to (Lima&Steury 2005). Thus prey are not unresponsive food items to be found and eaten by the predator, but they respond to the presence of predators by adjusting when and where to feed, by increasing their vigilance or searching for safer habitats in order to evade being killed. In this sense, predator prey interactions are a behavioral response game where predators try to find prey, and prey are trying to avoid their predators (Sih 2005). The outcome of this game is influenced by constraints, costs, and benefits. Costs and benefits will depend on the rate at which predator and prey encounter each other and hence on population density. Both predator and prey are thereby influenced by internal and external constraints. An internal constraint may be the energetic state of the individual players - an energetically stressed individual will be ready to take higher risks than a well fed one - whereas the distribution of resources for the prey or patches with increased attack success for the predator describe external constraints. The question whether prey and predator will show positive (i.e. the predators win) or negative association (i.e. the prey win) will depend on the relative ability of the two to respond to each other, the relative cost of responding and the relative benefit of responding (Sih 2005).

Defining the risk of predation

In the context of predator-prey interactions it is important to clearly define predation risk. Formally the risk of predation is the probability of being killed by a predator per unit time. This term was further divided by Lima&Dill (1990) into the basic components of risk (sensu Holling 1959) represented as

$$P(death) = 1-exp(-\alpha dT),$$

consisting of the rate of encounter between predator and prey α, the probability of death given an encounter d, and the proportion of time spent vulnerable to an encounter T. The probability of an encounter depends on factors such as predator density and movement behavior but also on habitat structure and complexity. The probability of death given an encounter is composed of the probability of an encounter and the probability of an attack given an encounter. Finally the time spent vulnerable may depend on the duration a prey is active or the time spent away from protective cover (Lima&Dill 1990). All three components are assessable and potentially manipulated by both predators and prey and overall predation risk thus varies over space and time.

In practice it is often difficult to clearly identify the individual components of risk and hence most empirical studies looking at the response of prey to predators use only one component to define predation risk (but see Hebblewhite et al. 2005a). For instance some studies use predator density (e.g. Anderson et al. 2005, Mao et al. 2005, Fortin et al. 2005) or predator habitat use as a proxy for spatial variation in predation risk (e.g. Whittington et al. 2011, Bastille-Rousseau et al. 2015), whereas others use the distribution of kills (e.g. Samelius et al. 2013, Lone et al. 2014). Finally, the third approach looks mainly at the time component of predation risk, testing how prey adjust their foraging time depending on the risk of predation (e.g. Brown et al. 1992, Kotler et al. 1992). All three approaches can give valuable insights into the behavioral response game of predators and prey but they may yield different results. Not all prey species will necessarily respond to all three components of risks and the relative importance of the different components will depend on the type of prey, the type of predator and the environmental context (Lima&Dill 1990). The best approach for a given study is therefore dependent on the particular questions that are asked, and will differ from case to case.

Spatial and temporal variation in predation risk

Predation risk varies both in space and time. Temporal variation in risk is dependent on predator space use (presence or absence) as well as on external factors such as light conditions or snow cover, which may change the success rate of a predator (Lima&Dill 1990). On the other hand, spatial variation in risk is more a function of predator habitat selection and specific habitat features associated with varying probability of death given an encounter. In this context, the risky times hypothesis is concerned with the response of prey to temporal variation in predation risk as a function of predator presence or absence, whereas the risky places hypothesis predicts that prey assess predation risk by the long-term level of risk associated with particular habitat features (Creel et al. 2008a). These two hypotheses are not mutually exclusive and are extended by the risk allocation hypothesis, which predicts that the optimal level of antipredator behavior during a pulse of high or low risk should depend on the long-term background level of risk (Lima&Bednekoff 1998).

The risk allocation hypothesis makes the counterintuitive prediction that in areas of high background level of risk, optimal antipredator behavior (such as vigilance) should decrease for both, situations of high and low risk. This is, because the higher the background level of risk the more prey will be energetically stressed and hence the less can they invest in antipredator behavior even during high risk situations. Empirical studies have found mixed support for the risk allocation hypothesis and more research is required to better understand its general applicability (Ferrari et al. 2009).

The ecology of fear

Brown et al. (1999) formulated "the ecology of fear" in which fearful prey respond to the presence of predators thereby reducing their exposure to predation risk. In a scenario where prey have imperfect information on the whereabouts of their predators, the optimal amount of antipredator behavior depends on factors such as numbers of predators and prey or the internal state and feeding rate of the prey. The strength of antipredator behavior should increase with predator numbers and concurrently reduce the catchability of the prey. Brown et al. found that such mechanisms should dampen population fluctuations of both predators and prey: increasing predator numbers results in warier and less catchable prey – and when predator numbers decrease again so should the optimal level of antipredator behavior which increases again the catchability and success rate of predators. In theory, such systems have been found to be highly stable (Brown et al. 1999, Creel et al. 2008b).

Consumptive and non-consumptive predation effects

In the ecology of fear framework, predators affect prey demography via two mechanisms: Consumptive effects (CE) and non-consumptive effects (NCE). CE act on prey numbers directly and are a function of the functional and numerical response of the predator to prey density. The overall predation rate is then defined as the percentage of the prey population killed per unit time. NCE are indirect fitness costs of prey resulting from costly antipredator behavior. These behaviors reduce the amount of time available for feeding or force animals to forage in safer but less productive habitat. Ultimately, NCE alter prey demography by reducing long-term survival and reproduction. A growing body of literature shows that NCE can be as important in shaping predator-prey dynamics as CE and may even act in the total absence of direct predation. In fact, CE and NCE are likely to be negatively correlated because it is the purpose of antipredator behavior to reduce direct CE (Creel et al. 2008b). The optimal level of antipredator behavior therefore depends on the effectiveness of the antipredator behavior and the associated relative fitness costs with respect to the CE. Thus there exists a tradeoff between CE and NCE and if antipredator behavior is effective in reducing the risk of predation prey should invest more into

the latter whereas if antipredator behavior is largely ineffective, prey should invest more time into energy acquisition and largely ignore variation in predation risk.

Predator hunting mode and habitat domain

Schmitz (2005) proposed that the strength of NCE in predator-prey systems is shaped by the prey's habitat domain in relation to the predators hunting mode and habitat domain. The habitat domain is defined as the proportion of available microhabitat used and considers both the choice of the microhabitat as well as the extent of the spatial movement within the chosen microhabitat (Preisser et al. 2007). Predators can then be divided into three types depending on their hunting strategies: sit-and-wait predators which wait until the prey come to them (e.g. ant lion or praying mantis), ambush predators which wait and hunt from an ambush but move to new grounds when prey abundance falls below a certain threshold (e.g. wolf spiders, hawks, cats) and active predators that are always on the move and pursue prey over long distances (e.g. ladybird beetles, weasels, wolves). Preisser et al. (2007) tested the predictions from Schmitz (2005) that the combination of predator habitat domain and hunting mode could provide a framework for predicting the strength of NCE in predator-prey systems using a meta-analysis approach. There was only limited support for the importance of habitat domain but predator hunting mode proved to be a major determinant of the strength of NCE. They found that the largest anti-predator response and thus NCE can be expected when prey are faced with sit-and-wait and ambush predators, whereas for active predators only little or no NCE are expected. Preisser et al. (2007) explain their findings with the fact that actively hunting predators may present a persistent predation risk cue and the high costs associated with constant predator avoidance may force the prey to only respond to imminent threat, whenever a predator is directly encountered. Cues from sit-and-wait and ambush predators on the other hand may provide reliable information on predation risk which can be used to efficiently avoid an attack by the predator. Creel et al. (2013) however raise the concern that these findings may not hold for large vertebrate systems. The authors argue that active predators have high energetic costs of hunting and therefore hypothesize that the costs of avoiding such predators will also be large. Indeed, results from wolf-elk predator-prey systems (with wolves being actively hunting predators) from different studies were equivocal. Some studies found strong NCE in terms of significant reductions in elk reproduction (Creel et al. 2007, Christianson&Creel 2010) while other studies did not find NCE (White et al. 2011, Middleton et al. 2013). On the other hand, there is strong evidence for strong NCE of Canadian lynx (Lynx canadensis), an ambush predator on snowshoe hares (Lepus americanus) in the northern boreal forest (reviewed in Peckarsky et al. 2008). There is thus a need for further studies looking at large vertebrate predator-prey systems with different predator hunting modes and habitat domains to shed more light on the general mechanisms driving the dynamics of such systems.

Predator-prey interactions and trophic cascades

It has long been recognized that predators can indirectly affect other species than their prey when these species interact themselves with the prey (Oksanen et al. 1981, Lima 1998). Often such indirect effects on other species have been attributed mainly to the reduction of prey numbers through CE, but there are also many examples where these processes were driven by NCE (reviewed in Werner&Peacor 2003, Schmitz et al. 2004). Indirect effects of predators on other species mediated via their prey can even propagate through different trophic levels of food webs and cause trophic cascades (Carpenter 1985). Such trophic cascades have been found in many different systems ranging from aquatic to terrestrial ecosystems and in various taxonomic groups, ranging from plants and algae to vertebrates. A famous example of a trophic cascade comes from an experiment in north temperate lakes in the USA where changes in the numbers of the top predatory bass fish resulted in major changes in zooplankton density via intermediate players of the food web (Carpenter et al. 1987). While this trophic cascade was first attributed to CE, later studies revealed that NCE were important determinants of the observed cascading effects in the altered food webs (Peckarsky et al. 2008). More recent examples of trophic cascades come from wolf-elk systems in North America where wolves were found to affect plant recovery by changing the density and distribution of their main prey, the elk (Hebblewhite et al. 2005b, Ripple&Beschta 2007, Ripple et al. 2013). There is however an on-going debate about the importance of CE and NCE in these trophic cascades whereat some studies find evidence for a large contribution of NCE (reviewed in Ripple et al. 2013) while other studies don't (Kauffman et al. 2010). Irrespective of the main drivers, trophic cascades highlight the importance of top predators in ecosystem dynamics and have been used as arguments for the conservation of threatened large vertebrate carnivores across the globe (Ripple et al. 2014).

Multiple predators

Many prey species are eaten by more than one type of predator. Effects of multiple predators on the same prey may not be independent from each other (reviewed in Sih et al. 1998). The concurrent presence of multiple predators can reduce or enhance the overall risk of predation for the prey depending on the predator hunting mode, the antipredator behavior of the prey and the interaction between the predators.

Risk reduction can occur when two predators of the same prey interact with each other either by interference competition or intra-guild predation, or if the antipredator behavior of the prey is effective in reducing the risk of predation from both predators. Rosenheim et al. (1993) provide an example of risk reduction from two predators on aphid (Aphis) population growth. They found that aphids did better in the presence of two predators, predatory lacewings (Chrysoperla) and predatory bugs (Geocoris, Nabis and Zelus), than when only lacewings were present in the

system. This was because the predatory bugs also predated on the lacewings, therefore reducing the predation pressure on aphids.

On the other hand, risk enhancement occurs when avoiding one predator increases the risk of predation by another one, a phenomenon also called predator facilitation (Charnov 1976). This is especially true in the case of predators of different hunting mode or habitat domain. A famous example of predator facilitation was provided by Kotler et al. (1992), where gerbils (Gerbillus) were exposed to predation risk by vipers and owls. Vipers increase the predation risk in the bush whereas owls increased predation risk in the open. In the presence of only owls gerbils reduced their risk of predation successfully by reducing foraging in the open whereas in the presence of both predators gerbils were exposed to higher predation risk by owls as they were driven into the open by the co-occurring vipers (Kotler et al. 1992).

In addition, the activity and hunting strategy of predators themselves may depend on whether other predators feeding on the same prey co-occur or not (Matsuda et al. 1993). In this context, Embar et al. (2014) showed experimentally that vipers and owls, both predators of gerbils, adjust their hunting activity depending on whether the other predator is present or not. Again this shows that both, predator and prey interact dynamically in a behavioral response game where each player is trying to outsmart the other one.

The human dimension in predator-prey interactions

Areas of low human impact on the planet are becoming increasingly rare. As a consequence, nearly everywhere animals have to deal with human-altered environments (Sih et al. 2011). Living in areas of high human impact, such as the surroundings of human settlements, often comes with costs but at the same time brings some benefits. Agricultural land is often highly productive and may offer rich resources, e.g. for herbivores (Marshall and Moonen 2002) or for predators that feed on commensal species (e.g. on rodents; Pita et al. 2009). On the other hand, mortality risk in close proximity to humans is often increased due to various reasons such as traffic accidents (eg. Fahrig and Rytwinski 2009), poisoning (Marquez et al. 2013), or legal and illegal harvesting (eg. Corlett et al. 2007). Thus, living in human-altered environments often requires animals to tradeoff between high resource abundance and increased mortality risk. Mistakes in correctly evaluating habitat quality can turn human-altered environments into ecological traps or, the opposite, create undervalued resources if animals avoid good quality habitat (Gillroy&Sutherland 2007). Both mechanisms may result in local extinctions and the reduction of biodiversity in areas of high human disturbance.

There is a large body of literature describing behavioral adaptations of wildlife in response to different human activities. Such behavioral adaptations have been shown in both predators (e.g. Bunnefeld et al. 2006, Hebblewhite&Merill 2008, Northrup et al. 2012, Ordiz et al. 2012) as well as in herbivorous species (e.g. Sawyer et al. 2006, Benhaiem et al. 2008, Ciuti et al. 2012) and

may have similar impacts on population dynamics as NCE of predators on prey (Oriol-Cotterill et al. 2015). Given the large potential for human-wildlife conflicts for large predators and given their low densities, these species may be particularly vulnerable to a combination of CE (i.e. humans actively killing carnivores) and NCE in human-altered environments (Ripple et al. 2014). At the same time, important game species such as many ungulates all over the world are exposed to concurrent "predation pressure" by humans and their natural predators (e.g. Hebblewhite et al. 2005a, Nilsen et al. 2009, Melis et al. 2013). Thus, research which explicitly addresses the role of humans in predator-prey interactions is required to better understand ecosystem dynamics in human-dominated landscapes and how this affects predator-prey interactions.

Lynx-roe deer predator-prey interactions in a human-dominated landscape

It was the goal of this thesis to look at the behavioral response game of a large mammalian ambush predator and one of its main prey and to identify the key components involved in shaping habitat selection and risk avoidance of both players in a human-dominated landscape. The work presented here focused on the interaction of the Eurasian lynx (Lynx lynx) and the European Roe deer (Capreolus capreolus) and explicitly tested how humans affected these interactions. The study area was situated in the North-westerns Alps of Switzerland and covered roughly 1500km2 (center coordinates 46.559905 N, 7.513052 E, Figure 1) and ranged in altitude between 600m and 3500m. The entire study region is used intensively for recreational purposes (Pesenti and Zimmermann 2013). Besides outdoor tourism such as hiking and skiing, hunting is an important activity among local people. The roe deer population is hunted between October 1 and November 15 every year. Deer densities in the area is not known explicitly, but according to game wardens densities have substantially decreased since the reintroduction of the lynx in the 1970s. The lynx population in turn is well known from previous radio-telemetry studies (e.g. Breitenmoser and Haller 1993, Molinari-Jobin et al. 2007) and repeated camera-trapping censuses (e.g. Pesenti and Zimmermann 2013). Lynx density in the region was estimated at 2.05 independent lynx/100 km2 from a camera-trapping census in winter 2013/14 (Zimmermann et al. 2014). The lynx in this region prey mainly upon roe deer (36% of identified kills) and chamois (39%%; KORA, unpublished data). Other important prey species are hares Lepus sp. (10%), marmots Marmota marmota (7%), and red foxes (6%). Occasional depredation of livestock (mainly sheep) also occurs but is rare (1.5%).

Roe deer are the most abundant ungulate in Europe and occur at high densities in fragmented cultivated land where they are closely associated with forest edges at the interface of open habitat and forest (Danilkin 1996). Roe deer are selective feeders mainly feeding on forbs and shrubs. Habitat selection of roe deer is known to follow seasonal patterns and is strongly affected by snow cover (Danilkin 1996, Mysterud et al. 1999). In addition, habitat selection differs between day and night, especially in areas of high human disturbance (Danilkin 1996).

Lynx are ambush predators by the definition of Schmitz et al. (2004). They ambush their prey and have been found to be most successful at sites where the habitat offers a high degree of complexity and low visibility (Podgorski et al. 2008). Kill sites are often found close to forest edges that provide good feeding opportunities for the deer and at the same time offer cover for the lynx to approach its prey. At large spatial scales, lynx are attracted to areas of intermediate human impact due to the high prey abundance (Bunnefeld et al. 2006, Basille et al 2009, Bouyer et al. 2015). However, at smaller spatial scales lynx have been found to avoid proximity to human features (Basille et al. 2009).

Lynx predation alone or in combination with hunting was found to have considerable effects on roe deer population dynamics depending on the environmental context (Nilsen et al. 2009, Melis 2013). However, previous studies of NCE of lynx on roe deer in Sweden and Norway have not been able to identify any shifts in habitat use of roe deer in response to lynx predation risk (Samelius et al. 2007, Ratikainen et al. 2007) even though roe deer have been found to respond to the experimental spreading of lynx urine (Eccard et al. 2015, Wikenros et al. 2015). On the other hand, roe deer are known to alter vigilance behavior and habitat selection in response to human hunting (e.g. Benhaiem et al. 2008, Padie et al. 2015). In the end, there is a lack of knowledge of how roe deer trade off between lynx predation and human associated risks. The study system was ideal to look at the behavioral response game of an ambush predator and one of its main prey in a human-dominated landscape.

Data collection

The lynx data used in this study were provided by KORA (Koordinationsstelle für Raubtierforschung in der Schweiz) and were collected in the context of a study on olfactory communication in lynx during which 17 lynx were captured and equipped with GPS-GSM radio collars between 2011 and 2014.

In the same period, we captured and collared 70 adult and juvenile deer during winter using drive nets or box traps. An additional 74 roe deer fawns were captured during the fawning season between May and July. In total, we collared 144 roe deer of which 65 animals were equipped with a GPS collar. For the analyses presented in this work I focused exclusively on the GPS data from the 65 GPS collared roe deer.

Outline of this thesis

This thesis is structured into three chapters, preceded by a general introduction into the topic of predator-prey theory (current section) and a general discussion of the major findings in the end. In these three chapters I look at various aspects involved in shaping the space use patterns of an ambush predator and one of its main prey and characterize the spatiotemporal drivers of habitat selection and risk avoidance of both players in a human-dominated environment. By focusing on both predators and prey I identify different key components of the behavioral response game between Eurasian lynx and European roe deer.

In the first chapter I investigated how tradeoffs between risk avoidance and resource abundance in human-altered environments affect habitat selection of Eurasian lynx. In particular, I studied how spatial scale interacts with the intrinsic behavioral state (active vs inactive) of Eurasian lynx in shaping the response to temporal and spatial fluctuations in human activity and prey availability. I show that lynx tradeoff between anthropogenic risk and prey density by using areas of high prey density during times of low human disturbance. This tradeoff differs among lynx behavioral states and is dependent on the spatial scale considered. In the following two chapters I used the habitat selection model of active lynx as a proxy for lynx predation risk and tested how roe deer adjusted their time spent vulnerable to predation. I thereby assumed that roe deer will respond to habitat features associated with the long term probability of encountering a lynx but did not account for putative habitat differences in the probability of death given an encounter. In the third chapter however, I also tested whether roe deer respond to the probability of death given an encounter component of predation risk by lynx.

Harvesting is likely one of the major determinants of wildlife populations dynamics. Nonetheless, hunting is often not considered as an ecological force driving ecosystem processes. As mentioned above multiple predators of a single prey may positively or negatively interact with each other via their prey. The same may be true for hunters that compete with natural predators for the same prey. Predator facilitation has been shown in various multiple predator-prey system in different taxonomic groups, however, remarkably little attention has been paid to how behavioral changes in game species in response to human hunting may affect the susceptibility of these prey to their natural predators. In the second chapter I explored how roe deer trade off between hunting risk and lynx predation risk and whether hunting increases the deer's susceptibility to lynx predation. I found that roe deer avoid areas of high hunting risk during the hunting season at the expense of higher exposure to lynx predation risk. Furthermore, there was strong evidence that lynx increased their hunting effort and hunting success during this time period. I show in this second chapter that hunting can induce predator facilitation through behavioral changes in both predator and prey, resulting in superadditive mortality.

Ecological theory predicts that ambush predators exert stronger NCE than active predators as they provide more persistent cues about predation risk than their widely roaming counterparts.

While evidence comes from different taxonomic groups, evidence from large mammalian predator-prey systems is rare and equivocal. Thus in the third chapter, I focused on the occurrence and strength of NCE of lynx on roe deer and tested for knock on effects on deer survival. Prey response to spatial and temporal variation in risk can be investiagted under the risky places and risky times hypothesis. Thus, I tested how roe deer respond to long-term levels of lynx predation risk (risky places) and how their antipredator behavior changes under acute predation risk when a lynx is in close proximity (risky times). I also tested whether these NCE affected mortality other than lynx predation. I found strong NCE in roe deer in response to both risky places and risky times. Finally the observed NCE were strong enough to exert knock on effects on deer survival. These findings are in accordance with ecological theory predicting strong NCE of ambush predators on their prey and indicate the importance of considering the temporal aspect when looking at predator-prey interactions.

In the general discussion at the end of this thesis I discuss the findings and implications of the previous three chapters in the light of predator-prey ecology and propose directions for future studies in this field.

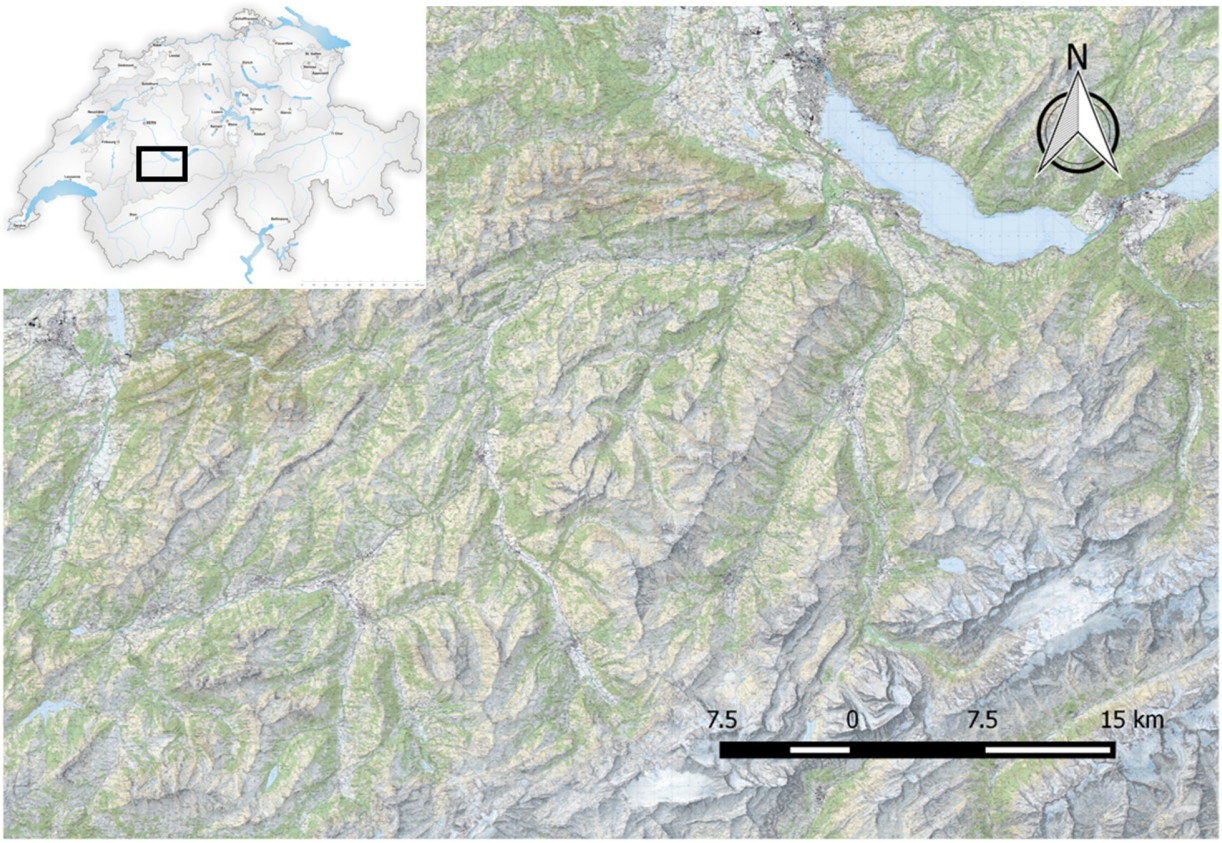


Figure 1 Map of the study site in the North-Western Alps of Switzerland

References

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management 69:298-310.

Basille, M., I. Herfindal, H. Santin-Janin, J. D. C. Linnell, J. Odden, R. Andersen, K. A. Hogda, and J. M. Gaillard. 2009. What shapes Eurasian lynx distribution in human-dominated landscapes: selecting prey or avoiding people? Ecography 32:683-691.

Bastille-Rousseau, G., J. R. Potts, J. A. Schaefer, M. A. E. Lewis, E. Hance, N. D. Rayl, S. P. Mahoney, and D. L. Murray. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography 38:1049-1059.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour 76:611-618.

Bouyer, Y., G. San Martin, P. Poncin, R. C. Beudels-Jamar, J. Odden, and J. D. C. Linnell. 2015. Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation 191:291-299.

Breitenmoser, U., and H. Haller. 1993. Patterns of Predation by Reintroduced European Lynx in the Swiss Alps. Journal of Wildlife Management 57:135-144.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399.

Brown, J. S., R. A. Morgan, and B. D. Dow. 1992. Patch use under predation risk. 2. A test with fox squirrels, sciurus-niger. Annales Zoologici Fennici 29:311-318.

Bunnefeld, N., J. D. C. Linnell, J. Odden, M. A. J. van Duijn, and R. Andersen. 2006. Risk taking by Eurasian lynx (Lynx lynx) in a human-dominated landscape: effects of sex and reproductive status. Journal of Zoology 270:31-39.

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. Vonende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68:1863-1876.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological Implications of Resource Depression. American Naturalist 110:247-259.

Christianson, D., and S. Creel. 2010. A nutritionally mediated risk effect of wolves on elk. Ecology 91:1184-1191.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B: Biological Sciences 279:4407-4416.

Corlett, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39:292-303.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23:194-201.

Creel, S., D. Christianson, S. Liley, and J. A. Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960-960.

Creel, S., J. A. Winnie, D. Christianson, and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. Animal Behaviour 76:1139-1146.

Creel, S., J. A. Winnie, Jr., and D. Christianson. 2013. Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: an example with wolves and elk. Ecology and Evolution 3:5189-5200.

Danilkin, A., and A. J. M. Hewison. 1996. Chapman and Hall Wildlife Ecology and Behaviour Series: Behavioural ecology of Siberian and European roe deer. Chapman and Hall Wildlife Ecology and Behaviour Series; Behavioural ecology of Siberian and European roe deer:xvi+277p-xvi+277p.

Embar, K., A. Raveh, I. Hoffmann, and B. P. Kotler. 2014. Predator facilitation or interference: a game of vipers and owls. Oecologia 174:1301-1309.

Fahrig, L., and T. Rytwinski. 2009. Effects of Roads on Animal Abundance: an Empirical Review and Synthesis. Ecology and Society 14.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 78:579-585.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.

Gilroy, J. J., and W. J. Sutherland. 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends in Ecology & Evolution 22:351-356.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834-844.

Hebblewhite, M., E. H. Merrill, T. L. McDonald, and E. Ranta. 2005a. Spatial Decomposition of Predation Risk Using Resource Selection Functions: An Example in a Wolf-Elk Predator-Prey System. Oikos 111:101-111.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005b. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Ent 91:293-320.

Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91:2742-2755.

Kotler, B. P., L. Blaustein, and J. S. Brown. 1992. Predator facilitation – the combined effect of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici 29:199-206.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions - What are the ecological effects of anti-predator decision-making? Bioscience 48:25-34.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. American Naturalist 153:649-659.

Lima, S. L., and L. M. Dill. 1990. Behavioral Decisions Made under the Risk of Predation - a Review and Prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68:619-640.

Lima, S. L., and T. D. Steury. 2005. Perception of Predation Risk: The Foundation. Pages 166-188 in P. Barbosa and I. Castellanos, editors. Ecology of Predator-Prey Interactions. Oxford University Press.

Lone, K., L. E. Loe, T. Gobakken, J. D. C. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos 123:641-651.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691-1707.

Marquez, C., J. Mario Vargas, R. Villafuerte, and J. E. Fa. 2013. Risk mapping of illegal poisoning of avian and mammalian predators. Journal of Wildlife Management 77:75-83.

Marshall, E. J. R., and A. C. Moonen. 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture Ecosystems & Environment 89:5-21.

Matsuda, H., P. A. Abrams, and H. Hori. 1993. The effect of adaptive antipredator behavior on exploitative competition and mutualism between predators. Oikos 68:549-559.

Melis, C., E. B. Nilsen, M. Panzacchi, J. D. C. Linnell, and J. Odden. 2013. Roe deer face competing risks between predators along a gradient in abundance. Ecosphere 4.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023-1030.

Molinari-Jobin, A., F. Zimmermann, A. Ryser, P. Molinari, H. Haller, C. Breitenmoser-Wursten, S. Capt, R. Eyholzer, and U. Breitenmoser. 2007. Variation in diet, prey selectivity and home-range size of Eurasian lynx Lynx lynx in Switzerland. Wildlife Biology 13:393-405.

Mysterud, A., L. B. Lian, and D. O. Hjermann. 1999. Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1486-1493.

Nilsen, E. B., J. M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. van Laere, and J. D. C. Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. Journal of Animal Ecology 78:585-594.

Northrup, J. M., J. Pitt, T. B. Muhly, G. B. Stenhouse, M. Musiani, and M. S. Boyce. 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. Journal of Applied Ecology 49:1159-1167.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240-261.

Ordiz, A., O.-G. Stoen, S. Saebo, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation 152:21-28.

Oriol-Cotteril, A., M. Valeix, L. G. Frank, C. Riginos, and D. W. McDonald. 2015. Landscapes of coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124:10.

Padie, S., N. Morellet, A. J. M. Hewison, J.-L. Martin, N. Bonnot, B. Cargnelutti, and S. Chamaille-Jammes. 2015. Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos 124:1536-1546.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416-2425.

Pesenti, E., and F. Zimmermann. 2013. Density estimations of the Eurasian lynx (Lynx lynx) in the Swiss Alps. Journal of Mammalogy 94:73-81.

Podgorski, T., K. Schmidt, R. Kowalczyk, and A. Gulczynska. 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica 53:97-110.

Preisser, E., J. Orrock, and O. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. Ecology 88:2744-2751.

Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138:514-519.

Ripple, W. J., R. L. Beschta, J. K. Fortin, and C. T. Robbins. 2013. Trophic cascades from wolves to grizzly bears in Yellowstone. Journal of Animal Ecology:n/a-n/a.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343:151-+.

Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96:439-449.

Samelius, G., H. Andren, P. Kjellander, and O. Liberg. 2013. Habitat Selection and Risk of Predation: Re-colonization by Lynx had Limited Impact on Habitat Selection by Roe Deer. PLoS ONE 8:1-8.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter Habitat Selection of Mule Deer Before and During Development of a Natural Gas Field. The Journal of Wildlife Management 70:396-403.

Schmitz, O. J. 2005. Behavior of predators and prey and links with population level processes. Pages 256-278 in P. Barbosa and I. Castellanos, editors. Ecology of Predator-Prey interactions. Oxford University Press.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153-163.

Sih, A. 2005. Predator-Prey Space Use as an Emergent Outcome.in P. Barbosa and I. Castellanos, editors. Ecology of Predator-Prey Interactions. Oxford University Press.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350-355.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367-387.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.

White, P. J., R. A. Garrott, K. L. Hamlin, R. C. Cook, J. G. Cook, and J. A. Cunningham. 2011. Body condition and pregnancy in northern Yellowstone elk: Evidence for predation risk effects? Ecological Applications 21:3-8.

Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology 48:1535-1542.

Zimmermann, F., D. Foresti, J. Bach, N. Dulex, C. Wuersten-Breitenmoser, and U. Breitenmoser. 2014. Abundanz und Dichte des Luchses in den Nordwestalpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2013/14.

Chapter 1
Spatial scale and behavioral state interact in shaping temporal dynamics of habitat selection in Eurasian lynx

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In revision from Oikos

Abstract

In human-altered environments, many large predators have to tradeoff between food availability and risk avoidance because prey densities are often highest where resources are abundant but human-induced mortality high. This tradeoff between risk avoidance and resource abundance can turn human-altered environments into ecological traps.

In this study, we investigated how tradeoffs between risk avoidance and resource abundance in human-altered environments affect habitat selection of Eurasian lynx (*Lynx lynx*), whose main prey in Central Europe, the European roe deer (*Capreolus capreolus*), thrives in close proximity to humans. Specifically, we asked how behavioral state (long-distance versus short-distance movements) affects time-dependent habitat selection at different spatial scales.

Using broken-stick models to separate movement data into long-distance and short-distance movements, and ordinary resource selection functions as well as step selection functions to investigate habitat selection, we show that behavioral state together with environmental factors acting at different temporal and spatial scales determine space use patterns of Eurasian lynx. Lynx avoided humans during the day but preferred areas of higher prey density during the night. Additionally, lynx avoided the temporary high human disturbance during hunting season by moving to higher altitudes. Both intensity and temporal dynamics of habitat selection differed among spatial scales. Furthermore we found risk avoidance to be most important during short-distance movements whereas prey-related variables were most crucial during long-distance movements. Altogether these results provide clear evidence that lynx respond dynamically to spatiotemporal variations in human disturbance and are thus able to cope with human-altered environments.

Our study illustrates that understanding predator space use requires habitat selection models that incorporate behavioral state and temporal dynamics of risk and resource distributions. Improving our understanding of how predators use their habitat and respond to human disturbance will help take the appropriate actions to ensure the preservation of ecosystem functioning in human-dominated landscapes.

Keywords: human-altered environment, risk avoidance, step selection function

Introduction

Human impact has reached almost every corner of our planet, and areas of low human impact are becoming increasingly rare. As a consequence, nearly everywhere animals have to deal with human-altered environments (Sih et al. 2011). Living in areas of high human impact, such as the surroundings of human settlements, often comes with costs but at the same time brings some benefits One of the costs of living in proximity to humans is an increased mortality risk, for instance due to traffic accidents (eg. Fahrig and Rytwinski 2009), collision with power lines (Rioux et al. 2013), poisoning (Marquez et al. 2013), and legal and illegal hunting (eg. Corlett et al. 2007). On the other hand, human-altered environments also have their benefits (Sih et al. 2010). Agricultural land is often highly productive and may offer rich resources, e.g. for herbivores (Marshall and Moonen 2002) or for predators that feed on commensal species (e.g. rodents; Pita et al. 2009). Proximity to human features may also offer shelter and protection (Zahn 1999).

Because of these costs and benefits, living in human-altered environments is associated with tradeoffs. This is especially true for large predators (Oriol-Cotteril et al. 2015). Many prey species of large predators occur at higher densities in proximity to humans (Linnell et al. 2005), yet this is also where the predators suffer from high human induced mortalities because people are afraid of large predators or compete with them for resources. This tradeoff between risk taking and resource abundance can turn human-altered environments into ecological traps (Bunnefeld et al. 2005).

Human-associated risks and resources vary over space and time in the same ways as other risks and resources. For example, a crop field may attract prey during the growing period of the crop but less so at other times, or a site may be risky during the day but safe during the night. As a consequence, habitat selection of predators may vary depending on season and time of day (eg. Belotti et al. 2013, Ordiz et al. 2012).

Habitat selection occurs at different spatial scales. Johnson (1980) divided habitat selection - or more generally, resource selection of animals - hierarchically into different orders depending on spatial scale. First order selection refers to the distribution of the species, second order selection determines the home range of an individual, third order selection describes selection of a patch within the home range (referred to as home range scale), and fourth order selection describes selection within patches (referred to as patch scale). When animals move in space, they have to take decisions at different scales (Boyce 2006). Often, selection at one scale may be different or even reversed at another scale. As an example, at the home range scale an animal may heavily depend on forest because it offers hiding places and protects from adverse weather conditions. At the patch scale, however, the animal may select areas close to forest edges because this is where it finds its food.

Animal decision-making not only depends on extrinsic habitat features but also on intrinsic factors. For example, habitat selection of animals differs depending on the behavioral state

(Roever et al. 2014). An individual looking for a safe site to rest has different habitat requirements than a hungry individual looking for food. Several studies have documented differing habitat selection depending on scale and behavioral state (eg. Johnson et al. 2002, Wilmers et al. 2013). For instance, a study of two toad species in Italy found that habitat type was most important for home range placement, whereas prey density and temperature mostly affected space use within home ranges (Indermaur 2009).

Our aim in this paper is to understand how the tradeoffs faced by large predators between risk taking and resource abundance affects their habitat selection in human-altered environments. To this end, we studied the Eurasian lynx (*Lynx lynx*), the largest felid predator in Europe. The main prey of Eurasian lynx in many parts of its range is the European roe deer (*Capreolus capreolus*), which is found at highest densities close to humans (Sunde et al. 2000, Jobin et al. 2000, Danilkin 1996). Human-related mortalities such as vehicle collision or hunting are the most important causes of death for lynx in many parts of Europe (Andrén et al. 2006, Schmidt-Posthaus et al 2002). Due to this positive correlation between prey availability and anthropogenic risks, areas close to human presence are attractive sinks for Eurasian lynx in Europe (Bunnefeld et al. 2006, Basille et al. 2009).

Habitat selection of lynx is known to be scale dependent. At large scales, lynx are attracted to areas of intermediate human impact (Bunnefeld et al. 2006, Basille et al 2009, Bouyer et al. 2015), but at smaller scales, lynx avoid proximity to humans (Basille et al. 2009) and flee from approaching humans at distances between 8 and 250m depending on habitat (Sunde et al. 1998). Moreover, a recent study from Norway showed that space use of lynx at the home range scale also depends on intrinsic behavioral state: human avoidance was higher during resting and feeding bouts than during long-distance movements (Bouyer et al. 2015). Hence, considering behavioral state is essential when studying habitat selection in lynx.

In this study, we investigate how behavioral state affects time-dependent habitat selection of Eurasian lynx in human-altered environments. We compared space use patterns at the home range and patch scale for two behavioral states, namely long-distance and short-distance movements, and made the following three predictions: First, we expected lynx to respond to tradeoffs between anthropogenic risk and prey density by using areas of high prey density during times of low human disturbance. Second, we predicted that lynx will select areas in close proximity to humans at the home range scale because of high prey abundance and in turn respond to temporal fluctuations in anthropogenic risk at the patch scale. Under this prediction, selection of habitat variables associated with humans should be stronger but less temporally variable at the home range scale than at the patch scale. Finally, we predicted that lynx are more sensitive to human disturbance during short-distance than during long-distance movements, as we assumed small-distance movements to be associated with resting and feeding behavior during which sensory awareness may be reduced.

Methods

Study area

This study was conducted in the Northwestern Swiss Alps (NWSA). The study area covered roughly 1500km^2 (center coordinates 46.559905 N, 7.513052 E) and ranged in altitude between 600m and 3500m a.s.l. The region is populated by humans (33 inhabitants/km^2) with most human settlements situated at the valley bottoms. Valley bottoms and lower slopes have been deforested since the middle ages for agricultural use. Remaining forests (about 30% of the total area) are situated mostly on the higher slopes and are highly fragmented. The treeline lies between 1800m and 1950m. The entire region is used intensively for recreational purposes (Pesenti and Zimmermann 2013). Besides outdoor tourism such as hiking and skiing, hunting is an important activity among local people. The main hunting season starts in September on chamois *(Rupicapra rupicapra*) and red deer (*Cervus elaphus*), whereas roe deer hunting is restricted to a 6 week period in October and November. The 2.5 month hunting season is characterized by an increased frequency of road traffic on remote roads and people patrolling in remote places. Humans pose an important mortality risk for lynx in the study area through vehicular collisions and poaching (Schmidt-Posthaus et al. 2002).

The lynx population in our study area is well known from previous radio-telemetry studies (e.g. Breitenmoser and Haller 1993, Molinari-Jobin et al. 2007) and repeated camera-trapping censuses (e.g. Pesenti and Zimmermann 2013). Lynx density in the region was estimated at 2.13 independent lynx/100 km^2 from a camera-trapping census in winter 2011/12 (Zimmermann et al. 2012). The lynx in this region prey mainly upon roe deer (36% of identified kills) and chamois (39%%; KORA, unpublished data). Other important prey species were hares *Lepus sp.* (10%), marmots *Marmota marmota* (7%), and red foxes (6%). Occasional depredation of livestock (mainly domestic sheep) also occurred but was rare (1.5).

GPS data

Between 2011 and 2014 we captured 17 lynx (8 females and 9 males). All lynx captures were approved by the Federal Office for the Environment and the district veterinary office of the canton of Berne. The capture protocol for lynx is described in detail elsewhere (Vogt et al., submitted). In brief, lynx were captured by one of three methods: At fresh kills using foot snares or a remotely controlled teleinjection system (Ryser et al. 2005), or in large double-door live traps. Captured lynx were immobilized and equipped with GPS-GSM radio collars (Vectronics Aerospace GmbH, Lotek Wireless) and released at the site of capture.

GPS fix intervals ranged between one and nine hours, with a majority of intervals at three hours (48%; see section on step selection functions for a description on how we dealt with interval heterogeneity). The GPS error for this study was estimated at 8.8m *(± 8.6m SD; described*

in Vogt et al., submitted). Outliers, such as single isolated locations, were removed from the data set. Only adult and resident lynx were considered in this study. Data from three lynx were removed from the analysis because they were either ill or subadult individuals during the entire monitoring period. Furthermore, we removed all data points in December 2012 for one lynx which was ill and didn't move during that time, because these data severely affected subsequent model outcomes. Finally, for one male lynx we excluded 2 obvious excursions to another part of the Alps before it became resident in the study area. After data processing 19'796 locations from 14 individual lynx remained (6 females and 8 males). The number of locations per individual ranged between 415 and 2'425 comprising between 140 and 567 monitoring days per individual.

Lynx behavioral states and broken stick models

Lynx behavioral states

Our study aimed to investigate the effects of animal behavioral states on habitat selection. Lynx often feed on large prey items over several days (Sunde et al 2000, Molinari-Jobin et al. 2002). During this time lynx show very restricted movements mainly between resting and feeding sites. After giving up a kill, lynx may then move large distances in search for new prey (Schmidt 1999). Given this general pattern, we separated the data into short-distance movements and long-distance movements based on speed between consecutive locations (see below). We assumed long-distance movements to be mainly associated with hunting behavior and patrolling territory, whereas short-distance movements were assumed to represent mostly feeding and resting.

Habitat selection during feeding and resting are known to be different. During resting concealment is important whereas during feeding lynx are more restricted to kill sites which are characterized by both good stalking cover and high visibility (Podgorski et al. 2008). In addition to this spatial separation, resting and feeding also show some temporal separation. Lynx are mainly active between dusk and dawn with activity peaks during crepuscular hours; during daytime lynx can often be found resting (Schmidt 1999, Heurich et al. 2015). Because of this temporal separation of the two behaviors (resting mainly during the day and partly during the night, feeding mainly during crepuscular hours and partly during the night), these behavioral differences matter when conducting time-dependent habitat selection analyses.

Broken-stick model

To separate lynx movements into short-distance and long-distance movements, we applied a broken-stick model based on speed (Sibly et al. 1990, Johnson et al. 2002). A two-process broken-stick model assumes that two Poisson processes generate movement rates. To separate the data into the two processes, we first categorized the movement rates into arbitrary regular spaces.

Space length ranged between 0.1m/min and 2m/min in order to avoid empty categories that cause difficulties in the subsequent analysis of log-transformed data (see Sibly et al. 1990 for a detailed description). In a next step the log transformed frequencies of steps within each movement rate category were plotted against the movement rate categories (Sibly et. al 1990). A break point in the resulting curve shows the cutoff that separates the two processes that generate movement rates (Figure A1 in supplementary materials appendix 1). We determined the exact location of this break point using a simple maximization routine (see supplementary materials appendix 1 for a detailed description). Finally, we used equation 5 in Sibly et al. (1990) to calculate the optimal speed threshold for separating the two processes while minimizing the number of falsely assigned steps. Because we found that the movement rate was dependent on the fix interval we calculated two separate broken stick models, one for 1h fix intervals and a second one for longer fix intervals (see below and supplementary materials appendix 1 for a detailed description).

Habitat variables

We included habitat variables in our study that had previously been identified as related to human activity and roe deer abundance (table 1). The density of buildings and the proximity to roads are habitat variables directly associated with human activity. Other habitat variables such as habitat type (forest vs unwooded land), distance to forest edge or altitude are indirectly correlated with human activity as settlements are situated in deforested valley bottoms. At the same time roe deer occur at particularly high densities on fragmented cultivated land where they are closely associated with forest edges at the interface of open habitat and cover (Danilkin 1996). Steep slopes have been associated with low human activity in previous studies and may serve as a refuge for roe deer (Zimmermann et al. 2002, Basille et al. 2009). Finally southern exposed slopes may be preferred by ungulates during winter because this is where snow cover first disappears (e.g. Plank 2013).

GIS-layers for assigning habitat attributes to GPS locations were provided by the federal office of topography (Swisstopo). Vector layers included habitat type, roads and buildings (swissTLM^{3D} 2013). We summarized habitat type into two categories: Forests, open forests, scrubland, and hedges were categorized as forest habitat. Everything else, i.e. agricultural land, alpine meadows, settlement area or rocky habitat was categorized as open habitat. We categorized habitat types into open and forest habitats, because most habitats other than forest and agricultural land were very rare (<3%) or unspecified in the GIS-layer except for rocky habitat (12%). However, preliminary analysis revealed that selection of the latter followed very closely selection of other open habitats (results not shown). For the analysis of habitat type we used forest as the reference category and modelled selection of open habitat.

We used building density and distance to roads as indicators of human disturbance (Zimmermann et al. 2002). We restricted our analysis to small roads (<=4m) as these were the most common road type in the study area. To calculate building density, we used a negative exponential smoothing kernel that decreased rapidly with distance from the building (kernel density of a single building dropped below 50% within 20m and disappeared beyond 100m; R-code by Björn Reineking, adapted from R-package EBImage - Pau et al. 2010). As a consequence, the distribution of the variable 'building density' was strongly right skewed and we applied a power transformation of the tenth root to achieve a better sample distribution of this variable (Quinn and Keough 2006). To account for the fact that selection/avoidance of roads might also depend on the proximity of buildings, we included an interaction term between distance to roads and building density in our models.

Lynx are known to hunt effectively near forest edges (Podgorski et al. 2008). For this reason we included distance to the closest forest edge as a covariate. An interaction between habitat type and distance to forest edge accounted for the fact that selection for proximity to forest edges may depend on whether the lynx is in the open or in the forest.

Finally we used a digital elevation model (swissALTI^{3D} 2013, DEM, 10mx10m resolution) to calculate altitude, slope and exposition. For exposition we only tested southern exposition against all other cardinal directions. All continuous covariates were standardized (mean of 0 and SD of 1). We used variance inflation factor (VIF) to test for multicollinearities between the explanatory variables. The highest variance inflation factor for continuous covariates was 1.86, which suggests that multicollinearity was not an issue in our models (Zuur et al. 2009).

Time dependence of habitat variables

One of the main foci of this study was to capture temporal dynamics of lynx habitat selection. We considered time of day and day of year as two different temporal scales. To model the diurnal and seasonal patterns of selection of different habitat covariates we followed the approach used in Forester et al. (2009). We included interaction terms between habitat covariates and four harmonics of time of day (TOD; calculated as decimal hours for each step) and day of year (DOY) respectively (TOD: $s_{1TOD}=\sin(2\pi t/24)$, $s_{2TOD}=\sin(4\pi t/24)$, $c_{1TOD}=\cos(2\pi t/24)$, $c_{2TOD}=\cos(4\pi t/24)$ and for DOY: $s_{1DOY}=\sin(2\pi t/365)$, $s_{2DOY}=\sin(4\pi t/365)$, $c_{1DOY}=\cos(2\pi t/365)$, $c_{2DOY}=\cos(4\pi t/365)$). This approach captures temporal fluctuations of habitat selection on a continuous scale.

Human activity differs markedly depending on the time of day or night, and season. For this reason we included time interactions for the four variables building density, distance to roads, open habitat, and slopes, and interactions with day of year for altitude and exposition. For the analysis we standardized time of day to Coordinated Universal Time (UTC). Difference to local time was 1 hour in winter (CET) and 2 hours in summer (CEST) due to daylight saving time.

Statistical analyses

To compare temporal dynamics of long distance and short-distance movements at the home range scale and at the patch scale, four habitat selection models were necessary, two at each spatial scale. Habitat selection at the two spatial scales was modeled differently.

Patch scale selection – Step selection functions

To model patch scale habitat selection of lynx we used step selection functions (SSF; Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). SSF are resource selection functions that take individual movement into account by comparing environmental attributes of realized animal locations with alternative random steps in a matched case-control design. The SSF took the exponential form

$$w(x)= \exp(\beta_1 x_1 \beta_2 x_2 + \ldots + \beta_n x_n)$$

where w(x) represents the step selection function score and the β's are the regression coefficients for the corresponding covariates x_n.

We used the empirical step length and turning angle distribution of lynx to draw the random steps (Forester et al. 2009). Forester et al. (2009) have shown that it is important to account for characteristics of animal movement (in the form of distance or direction travelled) in habitat selection models in order to get unbiased coefficient estimates. For this reason we included the step length as an additional covariate in the SSF models (Forester 2009, Warton and Aarts 2013). The SSF is estimated using conditional logistic regression, which assesses the resource selection of an animal conditional on a choice set of possible random steps. Conditional logistic regression does not allow to fit main effects for predictors that are constant within choice sets, which was the case for time of day and day of year (Allison 1991). Consequently we fitted temporal predictors only as interaction terms (table 1).

To account for serial autocorrelation in the data we applied a two-step SSF (Fieberg et al. 2010, Thurfjell et al. 2014). With this approach, separate models are first created for each animal and the coefficient estimates are then averaged over all individuals. This approach is sometimes favored over a generalized linear mixed model because it bypasses computational complexities of solving the likelihood (Craiu et al. 2011), and it solves the issue of complex correlation structures when combining used and available steps in one model, something that is difficult to achieve using standard modelling techniques (Fieberg et al. 2010). For model fitting we used the R-package TwoStepCLogit (Craiu et al. 2011).

For the generation of random steps we separated the steps into long distance and short-distance movements as described above. We excluded individuals with less than 200 locations after data separation. In the end, 8'258 steps of 12 lynx remained for the short-distance movement and 10'652 steps of 13 lynx for the long distance movement. Step length and turning

angles are dependent on the fix interval between consecutive fixes. To account for differences in step lengths and turning angles for different fix intervals we first regularized the data by excluding all steps with fix intervals greater than 6 hours (see Coulon et al. 2008 for a similar approach) and subsequently divided the remaining lynx steps into three fix interval categories of similar step length and turning angle distributions (<70min, 70-190min, 190-370min). Finally we drew 10 random steps and turning angles per used location from six different empirical distributions: 3 fix interval categories from 2 different behaviors. Step lengths and turning angles were drawn in pairs (Thurfjell 2014).

When feeding on a kill, lynx regularly switch between several different resting sites (K. Vogt, pers. communication). Nevertheless, an unknown proportion of steps assigned to short-distance movements may in fact represent random GPS error around a single resting location rather than true movements. In order to assess the effect of this on our analysis, we repeated the SSF for short-distance movements excluding steps smaller than the mean GPS error +1SD (17.4m; see above). This assumed that steps larger than this distance were true movements.

Habitat selection at the home range scale

For habitat selection at the home range scale we used the same 19'796 locations as for the patch scale analysis described above. We estimated lynx home ranges by drawing a buffer of twice the mean step length around the path of each individual lynx (all data pooled) and considered the resulting polygon as the home range of each lynx (Northrup et al. 2013, DeCesare et al. 2012). From this home range we drew 10 random locations per used lynx location and separated the data set into long distance and short-distance movements. Finally we built the resource selection functions using ordinary logistic regression. The RSF was of the form

$$w(x)= \exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n)$$

where w(x) represents the RSF score, β_0 is the intercept and the β's are the regression coefficients for the corresponding covariates ($x_1, \ldots, x_n$). We applied the same ratio of used to random locations for all animals which made the use of a random intercept for the individual lynx obsolete (Gillies et al. 2006). We tested for a functional response in selection of habitat type with a mixed model including a random slope for habitat type (Mysterud and Ims 1998, Beyer et al. 2010). Because the results were very similar to the simple logistic regression model, we only report the latter. Each random location was assigned a random time of day and day of year drawn from the observed lynx locations to account for the heterogenous sampling scheme of GPS fixes.

Serial autocorrelation

Animal movement data exhibit serial autocorrelation (Fieberg et al. 2010). In the patch scale models, the two-step SSF approach accounted for this autocorrelation by treating the individual as the sampling unit (Fieberg et al. 2010).

In the home range scale models, we used variance inflation methods to account for serial autocorrelation in the data (Newey and West 1987, Fieberg et al. 2010). Following the procedure in Roever et al. (2014) we calculated the corrected standard errors for the selection coefficients using the NeweyWest () function (Zeileis 2006) and lags between 10 and 60 time steps. Increasing the lag beyond 20 time steps (~60 hours) had only a minor effect on confidence intervals and did not affect model interpretation.

Model comparison

We modeled habitat selection separately for the two behaviors at the two different spatial scales. To facilitate comparisons, we used the same set of predictor variables for all four models (table 1). We started with a core model that included all predictors assumed to be important for lynx habitat selection (assessed from univariate resource selection models) and then increased model complexity by adding a) spatial interactions between predictors and b) temporal interactions between time/day of year (TOD and DOY) and the predictors. The core model included habitat type as a binary factor (open habitat=1, forest=0), distance to forest edge, distance to small roads, building density (power transformed; see above), southern exposition as a binary factor (southern exposed slopes=1, other=0), slope and altitude. For both slope and altitude we included a quadratic term to allow for non-linear dependencies of habitat selection. For this core model we then tested spatial interactions between habitat type and distance to forest edge as well as an interaction between road distance and building density. Finally, we added the temporal dependencies of predictor variables as described above. We did not fit temporal main effects for the home range scale models for the results to be comparable to the step selection functions (table 1).If any predictors turned out to be important for one of the four models, we kept them for further analysis in all models.

Model assessments and cross validation

We compared the four habitat selection models using model maximum likelihoods. Since individual model likelihoods of the first step in a two-step approach are additive (Fieberg et al. 2010) we were able to perform likelihood ratio tests between any pair of i) the core model, ii) the spatial interactions and iii) the temporal interactions (table 1). We did not use information criterion methods for model selection as in other habitat selection studies (e.g. Roever et al.

2014, Bastille-Rousseau 2015) because it is unclear how the appropriate number of degrees of freedom should be calculated in a two-step approach.

We visualized selection patterns revealed by the four models using pointwise confidence intervals for all predictor values (Fox 2003). Pointwise 95% confidence intervals of the home range scale RSF were obtained using the estimated variance-covariance matrix V(β) of the β-estimates and employing the approach described in Fox (2003, Section 2). We used the inflated V(β) matrix to account for serial autocorrelation (see above). For the SSF models, the V(β) matrix was estimated using a two-stage bootstrap (Efron and Tibshirani 1986). In order to keep the case-control design intact, realized steps and controls were sampled with replacement as entire groups (strata) in the first stage. In the second stage, ten controls were taken with replacement from the ten controls in the data set. 200 bootstrap iterations were performed in total. In the end we also estimated the relative importance of the individual model predictors as described in Ewald et al. 2014 (see supplementary materials appendix 1 for a detailed description).

We assessed the goodness of fit of the models using cross validation methods, repeatedly excluding 3 lynx as the test data set and using the remaining lynx to build the model (Boyce et al. 2002, Wiens et al. 2008). For the validation, we divided the RSF values of the random steps/locations into ten equal sized bins and used a moving average window of 3 to calculate the RSF values of the used steps/locations for the corresponding bin ranks. The Spearman rank correlation between the bin rank and the frequency of used steps per bin is a measure of the fit of the model (Wiens et al. 2008). We repeated this step 100 times, each time using a different training and test data set from all possible permutations (choosing 3 out of all lynx without replacements). In the end we tested the percentage of Spearman rank correlations that were above the critical value of 0.564 (which corresponds to a significant correlation on the α=0.05 level for n=10 pairs), and reported the mean correlation values over the 100 trials (Wiens et al. 2008). Large correlations can be interpreted as a good model fit.

Data processing

Data were managed using PostgreSQL 9.3.5 (PostgreSQL Global Development Group, 2014). All spatial intersections of GPS locations and habitat attributes were perfomed in PostGIS 2.1.3 (2014). Raster processing was done either using the R package raster (Hijmans 2015) or QGIS 2.8.1 Wien (Quantum GIS Development Team, 2014). All statistical analyses were performed in R (R core team, 2014).

Results

Lynx behavioral states

The broken-stick model used to separate the location data into long-distance and short-distance movements revealed an optimal threshold separating the fast and the slow process of 1.25m/min for the 1h GPS fix interval category, and 0.77m/min for the 3 and 6 hour categories. In other words, if a lynx moved further than 75m in a one hour step or further than 138m and 277m in a 3 to 6 hour step, respectively, its behavior was categorized as long distance movement, and short-distance otherwise. A χ^2-test for the two behaviors and the three fix interval categories revealed no differences in the ratio of large scale to small scale movements (χ^2_{2df}=4.33, p=0.12). Long distance movement was characterized by turning angles centered on 0 indicative of directed movement (Figure 1 a) whereas the turning angles for short-distance movements were centered on 180° (Figure 1 b). This may reflect on the one hand frequent movements between kill and resting sites during short-distance movements but on the other hand it may indicate that GPS error was large relative to the step length (Hurford et al 2009).

Habitat selection at two spatial scales

The likelihood ratio tests supported the most complex model including all temporal and spatial interactions for both behavioral states and both spatial scales (table 2). The cross validation analysis returned maximum correlation values for the SSF of the long distance movements as well as for the two patch scale habitat selection models (r_{CV100}=1) and somewhat smaller correlations for the SSF of the short-distance movements (r_{CV100}=0.81). For the latter, 95% of trials were above the critical value of 0.564 with a minimum value of 0.22 for one trial of three lynx. For the three other models, 100% of trials were above the critical value. This indicated a good fit between models and data.

To test the influence of GPS error on the SSF model of short-distance movements, we repeated the analysis by excluding steps smaller than what we assumed to be the threshold between true movements and random GPS error (17.4m; see Methods). Of all steps, 42 percent were smaller than 17.4m. The results of the SSF excluding all these steps were very similar to the model with the full data. Thus, in the following we only report the results of the SSF with the full data set.

Habitat type and distance to edge

Although all four models revealed that preference/avoidance of open habitat type followed a diurnal pattern, the amplitude and shape of the curves differed depending on behavior and spatial scale (Figure 2). In general, lynx avoided open habitat type most strongly in the middle of the day and least during the first half of the night. However, diurnal differences in avoidance of open habitat were more pronounced at the patch scale than at the home range scale. Avoidance

of open habitat type was not only scale dependent, but also depended on the distance to the closest forest edge: avoidance of open habitat became stronger the further away from the forest edge (see next paragraph).

At the home range scale, lynx clearly preferred to be near forest edges, both in the open as well as in the forest. The same was true for open habitat at the patch scale. However, inside forests at the patch scale there was no clear trend with very wide pointwise 95% CI 's (table 3 and Figure 3). The maximum distance to an edge inside forests was 400m (690m for random locations) compared to 1793m (4450m) in the open. Furthermore, 75% of all roe deer locations inside the forest were within 54m (57m) from the edge as compared to 113m (202m) in the open. The generally shorter distances to forest edge of both random and used locations inside the forest were a consequence of the small size of the forest patches.

Buildings and roads

Preference/avoidance of buildings and small roads followed similar patterns at both scales, but in general selection at the home range scale showed less diurnal fluctuations (Figure 4). During short-distance movements at the patch scale, avoidance of buildings and roads differed between day twilight and night. High building densities close to small roads were strongly avoided during day time hours and to a lesser extent also in the middle of the night. However, there was no avoidance during crepuscular hours. During the day, lynx strongly preferred low building densities far away from small roads. In contrast, selection patterns for the remaining three models were simpler. During the day high building densities were clearly avoided. During twilight and nighttime there were no clear preferences when lynx moved long distances. During short-distance movements, selection at the home range scale showed very little diurnal variation.

Altitude

Preference/avoidance of altitude followed a seasonal pattern with two peaks over the course of the year (Figure 5). The highest recorded lynx location was at 2610m and 50% of all locations were taken between 1286m and 1727m. Selection patterns were similar for both behaviors at the home range scale as well as for long distance movement at the patch scale. In all these three circumstances, preference for high altitude was strongest during late spring and early summer, then decreased during late summer and increased again during late fall and early winter. In the second half of winter lynx clearly avoided high altitudes. This contrasted with preference/avoidance of altitude at the patch scale during short distance movements, where the early winter peak was shifted to later in the year but the degree of selection was very uncertain.

Slope and exposition

Preference/avoidance of slope was similar for the two long distance movement models but differed markedly between the two short-distance movement models (Figure 6). For the long distance movement models the selection of slope followed a diurnal pattern. During daytime lynx preferred steep slopes and avoided flatter areas whereas at night steep slopes were avoided. In contrast, during short-distance movements selection of slope did not follow a diurnal pattern. During short-distance movements lynx preferred steeper slopes at the home range scale but there was almost no selection at the patch scale.

As was the case for altitude, preference/avoidance of southern exposed slopes strongly fluctuated over the course of the year (Figure 7). Lynx strongly preferred southern exposed slopes in winter and early spring (November-April) but showed no preference during the remaining months of the year. During short-distance movements, lynx were indifferent to slope exposition at the patch scale.

Relative importance of predictor variables

The relative importance of covariates in the four models depended on behavioral state as well as on the scale of selection (table 4; see supplementary materials appendix 1 for a list with all predictors). In general, habitat type (explaining between 21% and 30% of variance) and altitude (between 19% and 33%) were the most influential predictors. The relative importance of all other covariates, including those directly related to human activity (building density, distance to reads), was highly dependent on the behavior of the lynx and the scale of habitat selection (see table 4).

Table 1 Model structure for the two behaviors (long-distance and short-distance movements) at two scales (home range scale and patch scale). HT: habitat type, TOD: time of day, DOY: day of year.

Core model		
Habitat type	factor	open/forest
Edge distance	continuous	meter
Altitude	continuous	meter
Altitude sq	continuous	m^2
Slope	continuous	degree (1-90)
Slope sq	continuous	$degree^2$
Building density	continuous	unit $density^{0.1}$
Road distance	continuous	meter
Southern exposition	factor	south/non-south
Spatial interactions		
HT:edge distance	continuous	meter
Building:Road	continuous	density*meter
Temporal interactions		
HT:TOD	continuous	decimal time
Slope:TOD	continuous	decimal time
Building_density:TOD	continuous	decimal time
Road_dist:TOD	continuous	decimal time
Altitude:DOY	continuous	day of year
Southern exp:DOY	continuous	day of year

Table 2 Summary of the statistical analyses of the four habitat selection models. The last two columns show the results of the likelihood ratio tests (LRT) with the corresponding degrees of freedom (df) and the 100 cross validation trials from leaving out 3 lynx as a test data set for each trial. Cross validation trails were only done for the final models. r_{CV100}= mean Spearman rank correlation for the 100 cross validation trials. logit: logistic regression, clogit: conditional logistic regression.

Scale	Behavior	Statistical model	Autocorrelation correction	Model selection	LRT (df)	r_{CV100}
Home range						
	long-distance	logit	variance inflation	spatial interactions	p<0.001 (2)	-
				temporal interactions	p<0.001 (24)	1
	short-distance	logit	variance inflation	spatial interactions	p=0.001 (2)	-
Patch scale				temporal interactions	p<0.001 (24)	1
	Long-distance	clogit	two-step approach	spatial interactions	p<0.001(26)	-
				temporal interactions	p<0.001 (312)	1
	short-distance	clogit	two-step approach	spatial interactions	p<0.001 (24)	-
				temporal interactions	p=0.002 (288)	0.81

Table 3 Model outputs for the four habitat selection models (long distance and short-distance movements for both home range scale and patch scale). Positive regression coefficients correspond to preference whereas negative coefficients correspond to avoidance. Coefficients for year- and time -interactions have to be examined in combination and require plotting for interpretation. β= beta coefficients, SE= standard errors, HT: habitat type, AspectS: Southern exposition; ytsin, ytcos, ytsin2, ytcos2: year harmonics; tsin, tcos, tsin2, tcos2: time harmonics.

	Patch scale				Home range			
	Long distance		Stationary		Long distance		Stationary	
Variables	β	SE	β	SE	β	SE	β	SE
Habitat type	-0.70	0.16	-0.68	0.12	-0.57	0.07	-1.05	0.14
House density	-0.15	0.04	-0.01	0.07	-0.25	0.03	-0.31	0.05
Edge distance	-0.06	0.14	0.10	0.18	-0.39	0.11	-0.68	0.20
Road distance	0.19	0.07	0.35	0.10	0.08	0.04	0.20	0.07
Southern exp	0.31	0.05	0.03	0.06	0.31	0.05	0.46	0.08
Slope	0.10	0.04	-0.03	0.02	0.20	0.02	0.31	0.04
Slope sq	-0.08	0.02	0.00	0.01	-0.08	0.01	-0.07	0.02
Altitude	0.26	0.09	0.99	0.21	0.28	0.05	0.15	0.08
Altitude sq	-0.19	0.05	-0.09	0.10	-0.18	0.04	-0.32	0.06
HT:edge_distance	-0.69	0.25	-0.75	0.21	-0.27	0.14	0.01	0.29
House:Road	0.09	0.02	0.19	0.05	0.07	0.03	0.10	0.05
Step length	-0.06	0.08	-0.01	0.05				
Altitude:ytsin	-0.25	0.03	0.14	0.24	-0.25	0.06	-0.08	0.09
Altitude:ytcos	-0.48	0.10	0.07	0.27	-0.41	0.06	-0.45	0.10
Altitude:ytsin2	-0.34	0.04	-0.33	0.27	-0.45	0.06	-0.39	0.10
Altitude:ytcos2	-0.07	0.04	0.19	0.24	-0.13	0.06	-0.09	0.09
cover_tsin	-0.11	0.04	-0.19	0.06	-0.11	0.02	-0.01	0.03
Cover:tcos	0.29	0.05	-0.01	0.06	0.25	0.05	0.14	0.04
Cover:tsin2	0.10	0.04	-0.01	0.06	0.05	0.02	-0.03	0.03
Cover:tcos2	0.03	0.04	-0.14	0.06	-0.01	0.02	-0.02	0.03
Slope:tsin	0.15	0.03	0.06	0.03	0.10	0.02	0.01	0.02
Slope:tcos	-0.22	0.05	-0.08	0.03	-0.20	0.03	-0.12	0.03
Slope:tsin2	-0.03	0.02	-0.01	0.03	-0.03	0.02	0.03	0.02
Slope:tcos2	0.04	0.03	-0.04	0.03	0.01	0.02	-0.04	0.02
AspectS:ytsin	0.34	0.06	0.01	0.07	0.24	0.08	0.13	0.11
AspectS:ytcos	0.32	0.05	0.07	0.08	0.19	0.09	0.29	0.12

AspectS:ytsin2	0.10	0.04	0.07	0.07	0.07	0.09	0.03	0.11
AspectS:ytcos2	0.04	0.05	0.08	0.07	-0.01	0.09	-0.08	0.12
Road_dist:tsin	0.05	0.06	0.24	0.19	-0.02	0.02	0.00	0.02
Road_dist:tcos	-0.04	0.03	-0.08	0.14	-0.01	0.03	-0.06	0.03
Road_dist:tsin2	-0.05	0.03	-0.40	0.16	0.02	0.02	0.00	0.02
Road_dist:tcos2	-0.01	0.03	0.08	0.13	0.01	0.02	0.02	0.02
House_density:tsin	-0.11	0.03	-0.08	0.07	-0.07	0.02	0.03	0.02
House_density:tcos	0.16	0.03	0.14	0.07	0.21	0.03	0.09	0.03
House_density:tsin2	0.02	0.03	0.08	0.07	-0.02	0.02	-0.05	0.02
House_density:tcos2	-0.03	0.03	0.01	0.08	0.00	0.02	0.00	0.02

Table 4 Relative importance values for the predictors in the four core models (long distance and short-distance movements for both home range scale and patch scale). Relative importance is expressed as a value between 0 and 1 whereas the values of all predictors sum to 1. The higher the value the greater the importance of the predictor for the model.

	Patch-long distance	Patch-short-distance	Home range - long distance	Home range - short-distance
Habitat type	0.295	0.294	0.209	0.293
Distance to forest edge	0.086	0.253	0.051	0.045
Altitude	0.303	0.244	0.334	0.191
Slope	0.077	0.003	0.132	0.167
Southern exposition	0.113	0.001	0.096	0.137
Building density	0.07	0.034	0.165	0.132
Distance to roads	0.056	0.17	0.014	0.034

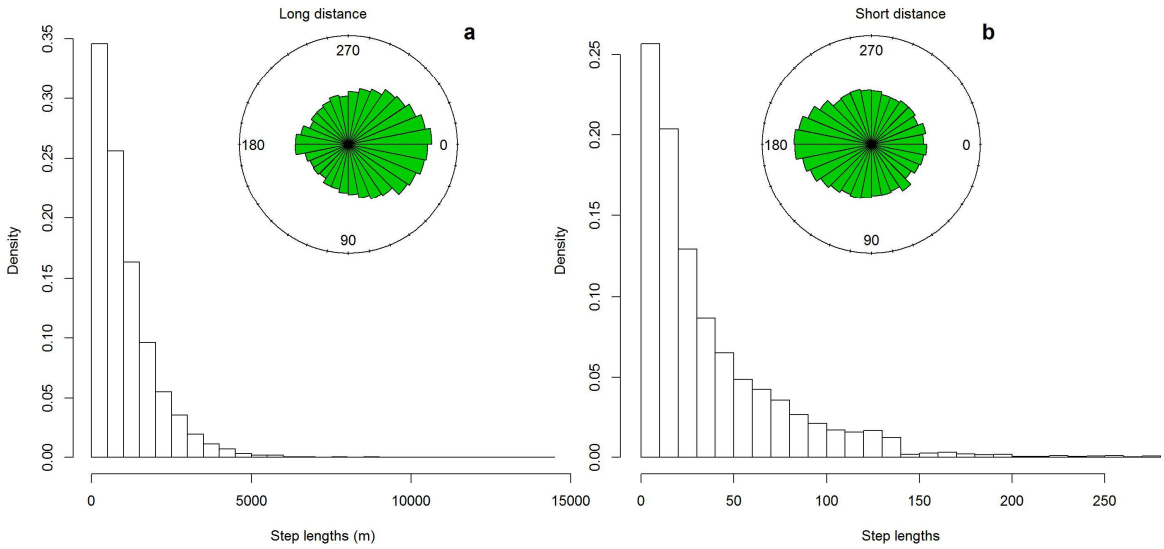

Figure 1 Distribution of step length (histogram) and turning angles (rose diagram) for a) long distance movements and b) short-distance movements.

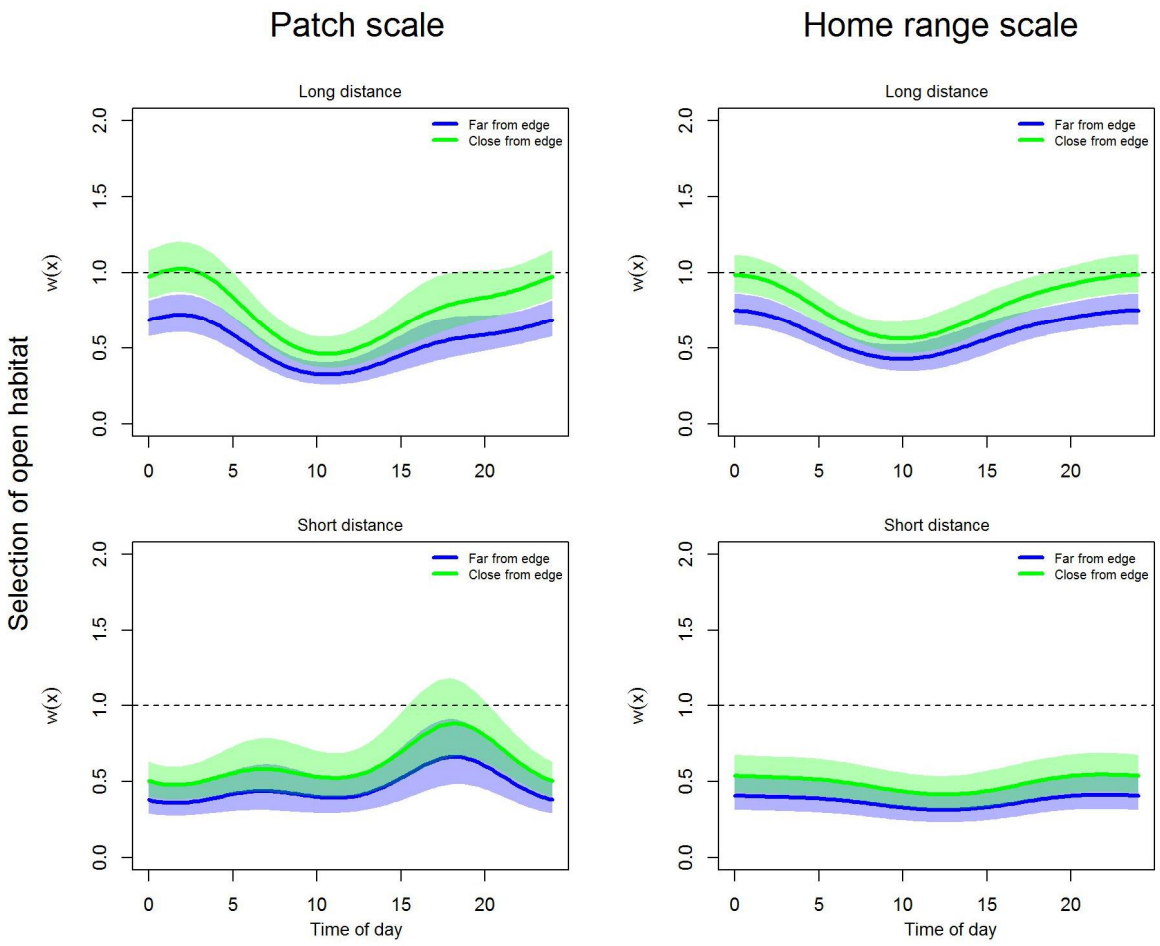

Figure 2 Time dependent selection of open habitat as a function of distance to forest edge for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). All panels show interactions between open habitat type and time of day while setting all other covariates to their mean (which is zero due to covariate centering) except for distance to forest edge. Green curves refer to the 25% quantile, blue curves refer to the 75% quantiles of distance to forest edge respectively. Blue and green shadings indicate the pointwise 95% confidence intervals for the respective curve. The dotted line for w(x)=1 represents no selection. As an example how to interpret these plots: The selection coefficient for open habitat during long distance movements at the patch scale reveals no preference or avoidance for open habitat close to forest edges between ~11pm and 5am (w(x)~1 for the green curve) whereas open habitat is clearly avoided during the day (w(x)<1). For locations far away from forest edges (blue curve) open habitat is avoided at all times, although to a lesser extent during the night. Because we used coordinated universal time (UTC), time curves are shifted by one (for central European time; CET) and 2 hours (for central European summer time; CEST) respectively with respect to local time. w(x): RSF or SSF score.

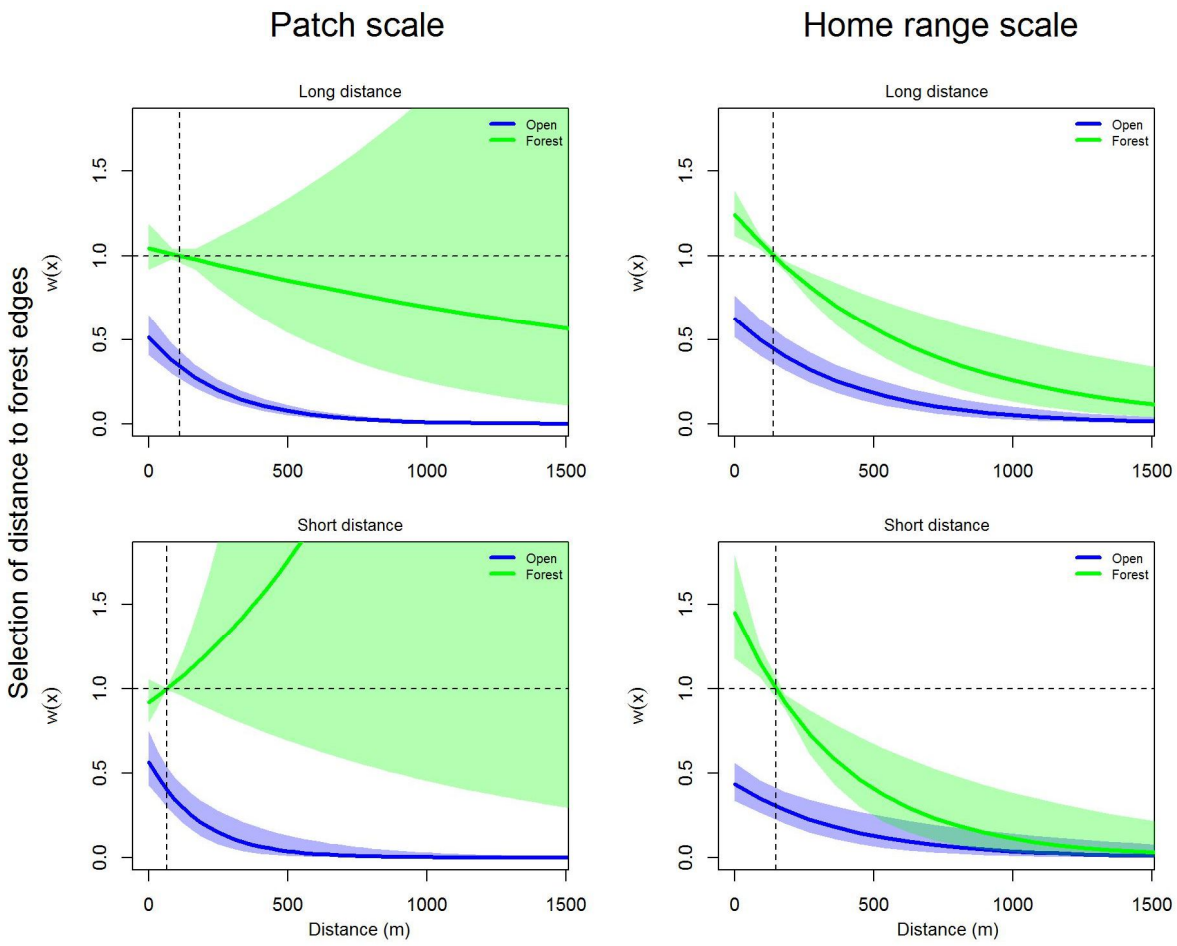

Figure 3: Selection of distance to edges in open habitat (blue curve) and in the forest (green curve) for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). Blue and green shadings indicate the pointwise 95% confidence intervals for the respective curves. The horizontal dotted line for w(x)=1 represents no selection. The vertical dotted line indicates the mean distance to forest edges for all lynx locations (the mean is set to zero and used as the reference for the analysis by covariate centering). w(x): RSF or SSF score.

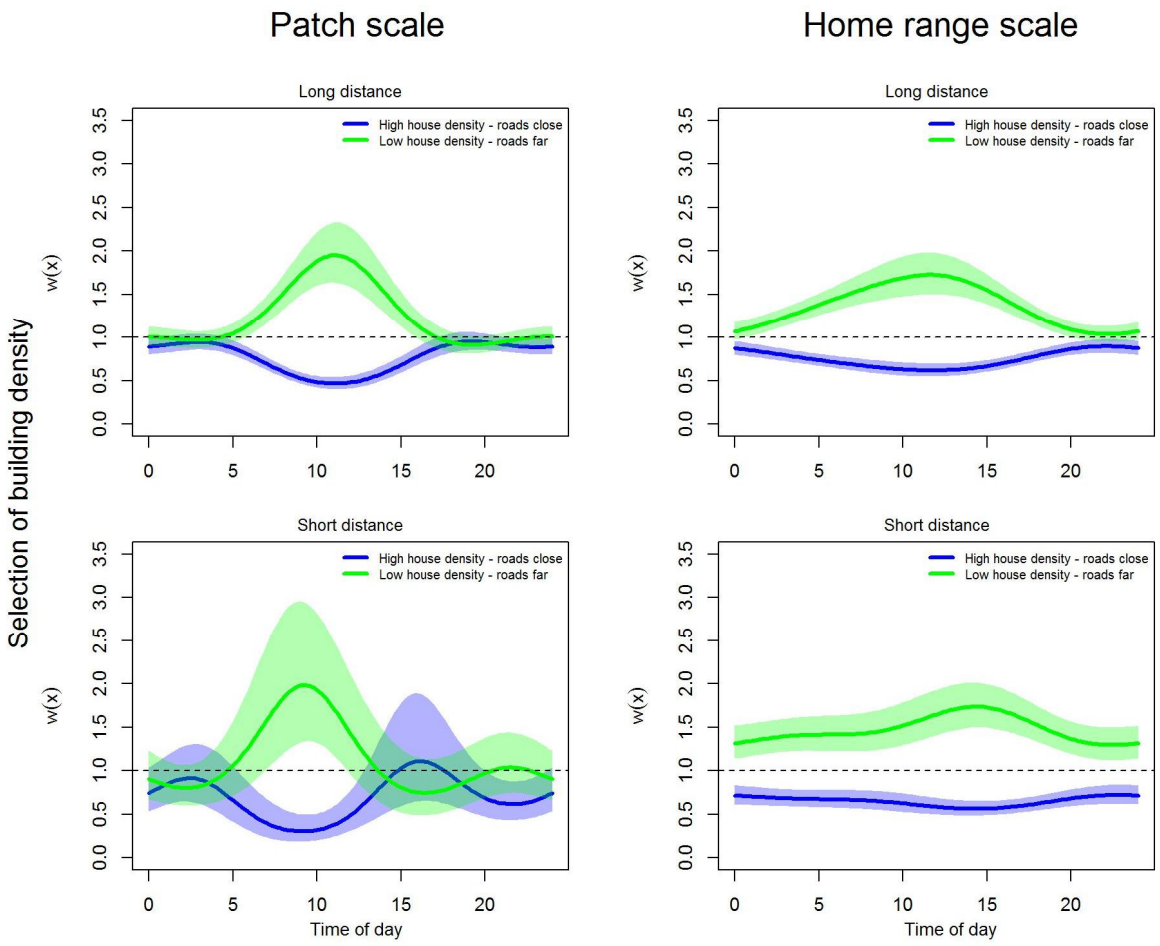

Figure 4 Time dependent selection of building density as a function of distance to roads for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). All panels show interactions between building density and time of day while setting all other covariates to their mean (which is zero due to covariate centering) except for distance to roads. Green curves refer to the 25% quantile of building density and 75% quantile for distance to roads, blue curves refer to the 75% quantiles of building density and 25% quantile for distance to roads. Blue and green shadings indicate the pointwise 95% confidence intervals for the respective curves. The dotted line for w(x)=1 represents no selection. Because we used UTC, time curves are shifted by one (CET) and 2 hours (CEST) respectively with respect to local time. w(x): RSF or SSF score.

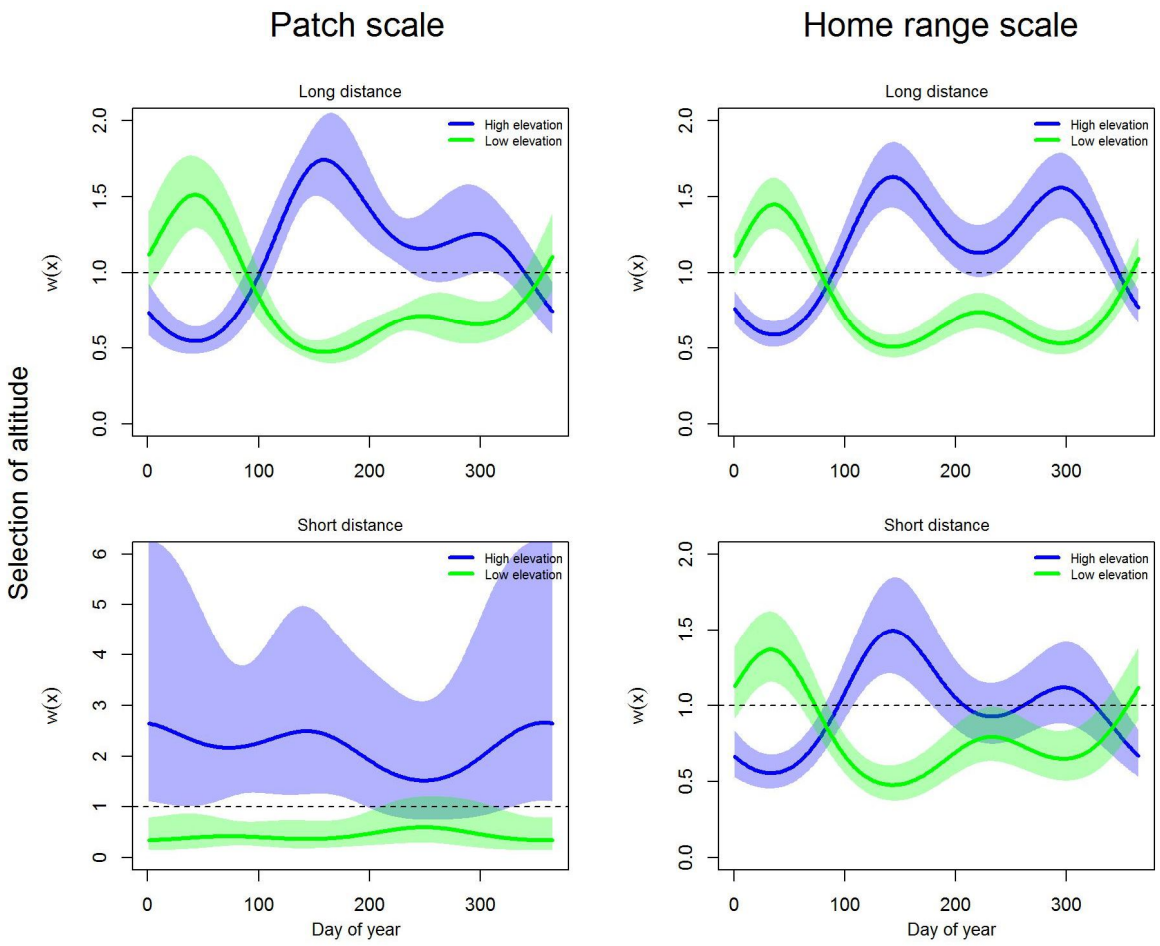

Figure 5 Seasonal habitat selection of altitude for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). The panels show interactions of altitude with day of year while setting all other covariates to their mean (which is zero due to covariate centering). Green curves refer to the 25% quantile, blue curves refer to the 75% quantiles for altitude. Blue and green shadings indicate the pointwise 95% confidence intervals for the respecting curves. The dotted line for w(x)=1 represents no selection. w(x): RSF or SSF score.

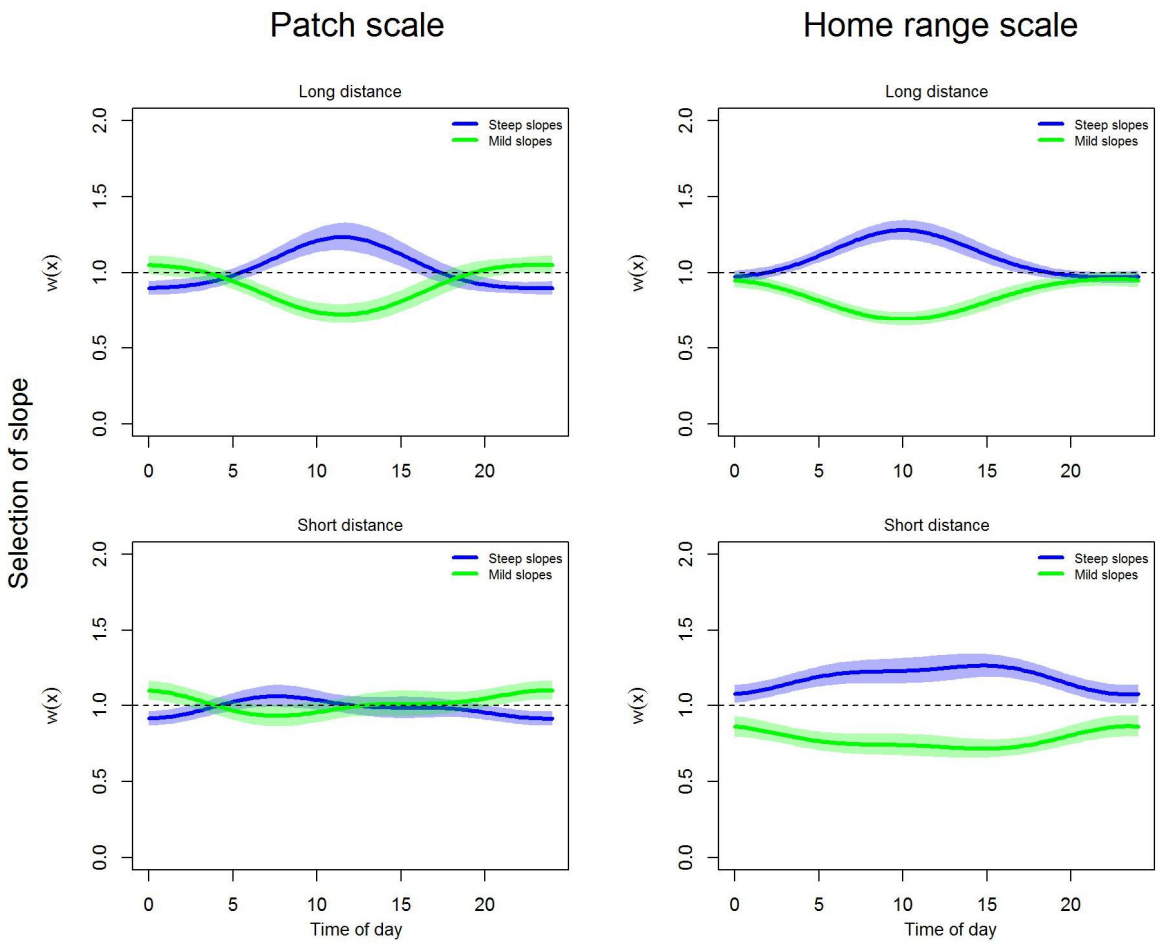

Figure 6 Time dependent selection of slope for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). All panels show interactions between slope and time of day while setting all other covariates to their mean (which is zero due to covariate centering). Green curves refer to the 25% quantile, blue curves refer to the 75% quantiles of slope (slope ranges between 0-90 degrees). Blue and green shadings indicate the pointwise 95% confidence intervals for the respective curves. The dotted line for w(x)=1 represents no selection. Because we used UTC, time curves are shifted by one (CET) and 2 hours (CEST) respectively with respect to local time. w(x): RSF or SSF score.

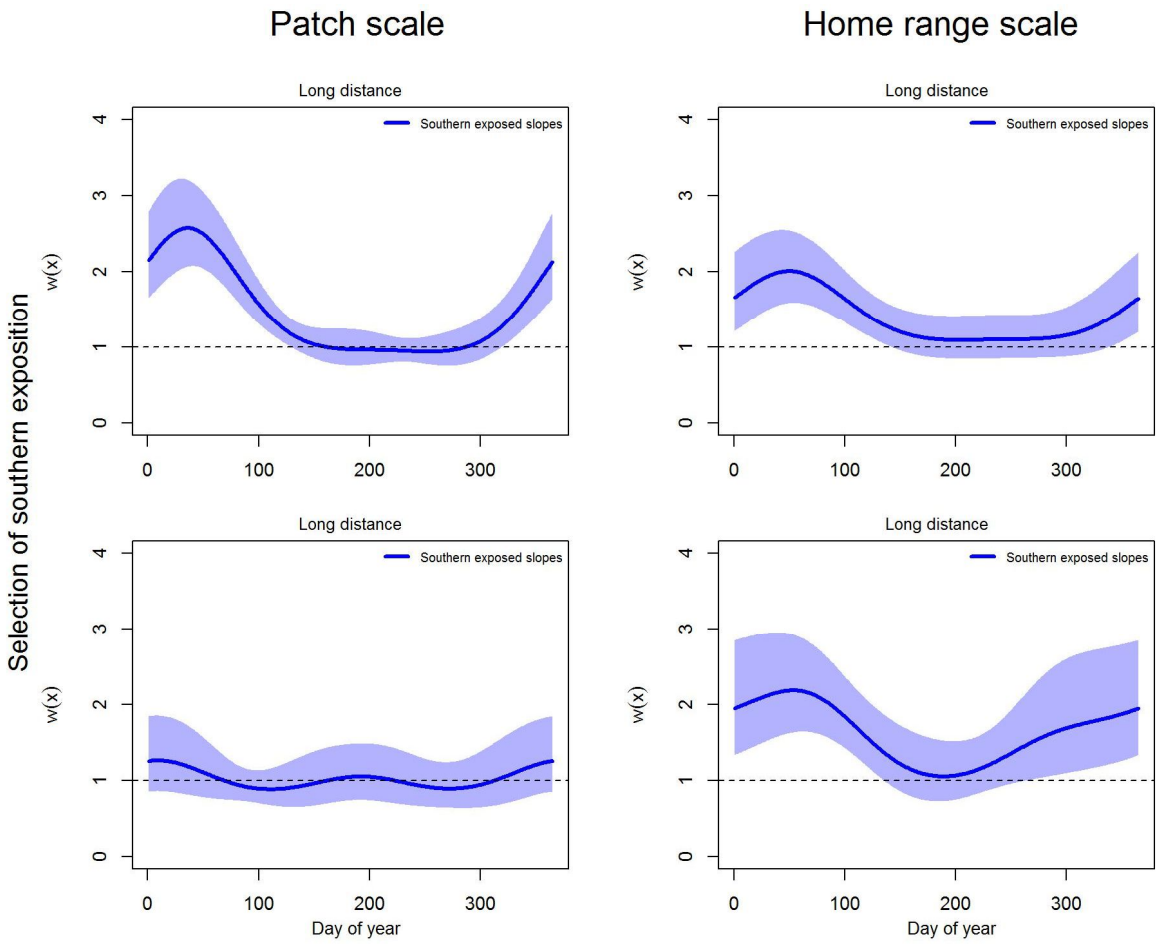

Figure 7 Seasonal habitat selection of southern exposed slopes for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). The panels show interactions of southern exposition with day of year while setting all other covariates to their mean (which is zero due to covariate centering; southern exposition is a binary variable with 1=southern exposition and 0=other exposition). Blue shadings indicate the pointwise 95% confidence intervals for the respective selection curves. The dotted line for w(x)=1 represents no selection. w(x): RSF or SSF score.

Discussion

In this study, we explored how behavior affects time-dependent habitat selection of Eurasian lynx at different spatial scales in human-altered environments. We used a broken-stick model to separate Eurasian lynx GPS locations into long-distance movements and short-distance movements and compared temporal dynamics of habitat selection between these two behavioral states at the home range scale (3rd order) and the patch scale (4th order). Our results indicate that Eurasian lynx take into account multiple factors acting at different temporal and spatial scales including their current behavioral state, resulting in complex habitat selection patterns.

Because we expected lynx to tradeoff between anthropogenic risk and prey density by using areas of high prey density during times of low human disturbance, we predicted i) that lynx habitat selection is temporally variable in response to fluctuations in human associated risk; ii) that lynx will select areas in close proximity to humans at the home range scale because of high prey abundance, but in turn respond more strongly to temporal fluctuations in human associated risk at the patch scale; and iii) that lynx are less sensitive to human disturbance when searching for prey (long distance movements) than otherwise.

In accordance with our first prediction, we found habitat selection of lynx to be highly variable over time, both on a daily and a yearly basis. For example, lynx responded to fluctuations in human disturbance by avoiding areas of high building densities during daytime, but not during twilight and nighttime when moving long distances and searching for prey (Figure 4). Basille et al. (2009) suggested the existence of attractive sinks for lynx close to humans where prey density is high but so is human-induced disturbance and mortality. The strong temporal variation over the course of the day in avoidance of habitat features associated with human presence suggests that lynx respond to this tradeoff: avoiding humans during the day but preferring areas of higher prey density during the night. Temporal variation in habitat selection in response to this tradeoff has also been demonstrated in other predators such as bobcats, brown bears and cougars (Van Dyke et al. 1986, George and Crooks 2006, Ordiz et al. 2012).

In addition to diurnal tradeoffs between human associated risks and food abundance, lynx also responded to seasonal variation in risk and prey availability. Selection of high altitudes showed two distinct peaks over the course of the year at both home range and patch scales (Figure 5). The summer peak is most likely related to increased prey availability at higher altitudes as lynx increasingly prey on marmots and young chamois during that time of the year. Another peak, however, coincides with the hunting season of chamois and roe deer between September and November. During that period of the year, disturbance of hunters in the study area is high. This manifests itself in increased numbers of vehicles and humans patrolling in remote places in the search for game. Lynx seem to avoid this temporary high disturbance during hunting season by moving to higher altitudes. In a similar context, Basille et al. (2009) found that female lynx

with kittens avoid high human disturbance when their offspring were still small. With increasing age of the kittens, avoidance gradually decreased. Together with our results, this shows that lynx respond flexibly both to fluctuations in anthropogenic risks and to their own vulnerability. It would be interesting to further investigate whether lynx hunting strategy or prey spectrum changes during the hunting period.

We predicted lynx to select areas of high prey density close to humans at the home range scale and in turn respond to temporal variation in risk and prey availability at the patch scale. Indeed, selection of forest edges was stronger at the home range scale than at the patch scale (Figure 3). At the same time, avoidance of building density and proximity to roads showed stronger diurnal variation at the patch scale than at the home range scale (Figure 4) and the same was true for avoidance of open habitat (Figure 2). Forest edges are attractive habitat for roe deer because they are associated with forests that provide cover but often also with agricultural fields, which provide rich foraging sites (Danilkin 1996). On the other hand, agricultural fields tend to be close to roads and human settlements. Hence, the observation that lynx have a strong preference for forest edges at the home range scale coupled with temporal avoidance of humans at the patch scale is in line with our expectations above. These results confirm findings from previous studies showing that lynx prefer areas of intermediate human activity and that lynx can tolerate human disturbance as long as there are enough forested areas for them to hide (Sunde et al. 1998, Basille et al. 2009).

Bouyer et al. (2015) have shown that vulnerability of lynx to human disturbance depends on behavioral state. Lynx are known to be most vulnerable during resting but tolerate much higher disturbance during long-distance movements. Our results confirm these findings and add an interesting temporal aspect. At the patch scale, lynx manifested the strongest avoidance of buildings and roads short-distance movements during daytime. At crepuscular hours, short-distance movements may frequently be associated with feeding behavior during which lynx are constrained to kill sites as they cannot drag their kills very far. Accordingly, lynx exhibited no avoidance of human-associated features at the patch scale during these hours of the day. Our results thus mirror the findings of Bouyer et al. (2015) that resting sites are situated in areas of lower human disturbance than kill sites. Altogether these results provide clear evidence that lynx respond dynamically to human disturbance according to their behavioral state.

However, our step selection function analysis revealed that the effects of behavioral state on habitat selection depended on the spatial scale. During feeding and resting, lynx are constrained by the location of their kills and habitat selection occurs at a finer scale than during long distance movements. For example, the observed differences in avoidance of human activity during short-distance movements at the patch scale (Figure 4) show that lynx may take habitat selection decisions at a very small scale. On the other hand, selection of slope and southern exposition clearly occurred at the home range scale whereas at the patch scale no selection was apparent. This indicates that these variables probably did not offer enough biologically meaningful variation

at this small scale to choose from. All in all, the spatial scale of habitat selection in lynx was not independent of the behavioral state.

We did not directly include prey data to understand habitat selection of lynx in this study. As highlighted by a recent study on Amur tigers in Siberia, taking the availability of all prey species into account improves the understanding of how prey occurrence shapes habitat selection of a predator (Petrunenko 2015). Unfortunately, we did not have detailed information about the distribution and density of all the important prey species in the area (roe deer, chamois, marmots, hares) and were thus unable to include this information in our models.

Our study emphasizes the importance of incorporating temporal dynamics of risk and resource distributions into habitat selection studies. Looking at time-dependent habitat selection of lynx during different behaviors at different scales revealed that habitat selection is never a simple one-dimensional process but incorporates decisions made at multiple spatial and temporal scales that influence each other as animals move through space. Future studies should include habitat selection models of prey species as well as information on prey density into temporally dynamic predator models in order to identify the proximate factors shaping predator habitat selection. Finally, it will be interesting to validate the association of different lynx behaviors (searching, resting, feeding) with the behavioral states used in this study using accelerometer data. Research in this direction will contribute to a better understanding of risk avoidance and resource selection of large predators in human-dominated landscapes.

In many parts of the world, conservation efforts to protect large carnivores are met with variable success (Treves and Karant 2003, Chapron et al. 2014, Ripple et al. 2014). Improving our understanding of how predators use their habitat and respond to human disturbance will help taking the appropriate actions for efficient conservation of these charismatic species and thereby contribute to the preservation of ecosystem functioning in human-dominated landscapes. Even though the Eurasian lynx is not threatened over the entire distribution of its range, in Central Europe lynx populations are small and fragmented, raising concerns about their long term persistence (Kaczensky et al. 2012). The results of our study, together with others, show that the Eurasian lynx is capable of adapting to a human-dominated landscape that is highly fragmented and densely populated (Sunde et al. 1998, Bunnefeld et al. 2005, Basille et al. 2009, Bouyer et al. 2015). The more serious challenge to ensure lynx population subsistence in Central Europe will be to reduce human induced mortalities in order to reverse population sinks into population sources. A better understanding of risk avoidance and resource selection of lynx represents one step towards this goal.

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References

Allison, P. D. 1991. Logistic regression using the SAS system - Theory and application. - Cary, NC: SAS Institute Inc.

Andren, H., et al. 2006. Survival rates and causes of mortality in Eurasian lynx (Lynx lynx) in multi-use landscapes. - Biological Conservation 131: 23-32.

Basille, M., et al. 2009. What shapes Eurasian lynx distribution in human-dominated landscapes: selecting prey or avoiding people? - Ecography 32: 683-691.

Bastille-Rousseau, G., et al. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. - Ecography 38: 1049-1059.

Belotti, E., et al. 2013. Foraging sites of Eurasian lynx Lynx lynx: relative importance of microhabitat and prey occurrence. - Wildlife Biology 19: 188-201.

Beyer, H. L., et al. 2010. The interpretation of habitat preference metrics under use–availability designs. - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2245-2254.

Bouyer, Y., et al. 2015. Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. - Biological Conservation 191: 291-299.

Boyce, M., et al. 2002. Evaluating resource selection functions. - Ecological Modelling 157: 281-300.

Boyce, M. S. 2006. Scale for resource selection functions. - Diversity and Distributions 12: 269-276.

Boyce, M. S., et al. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2213-2219.

Breitenmoser, U. and Haller, H. 1993. Patterns of Predation by Reintroduced European Lynx in the Swiss Alps. - Journal of Wildlife Management 57: 135-144.

Bunnefeld, N., et al. 2006. Risk taking by Eurasian lynx (Lynx lynx) in a human-dominated landscape: effects of sex and reproductive status. - Journal of Zoology 270: 31-39.

Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. - Science 346: 1517-1519.

Coulon, A., et al. 2004. Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual–based approach. - Molecular Ecology 13: 2841-2850.

Craiu, R. V., et al. 2011. Conditional Logistic Regression With Longitudinal Follow-up and Individual-Level Random Coefficients: A Stable and Efficient Two-Step Estimation Method. - Journal of Computational and Graphical Statistics 20: 767-784.

Danilkin, A. and Hewison, A. J. M. 1996. Chapman and Hall Wildlife Ecology and Behaviour Series: Behavioural ecology of Siberian and European roe deer. - Chapman and Hall Wildlife Ecology and Behaviour Series; Behavioural ecology of Siberian and European roe deer

DeCesare, N. J., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. - Ecological Applications 22: 1068-1083

Ewald, M., et al. 2014. LiDAR Remote Sensing of Forest Structure and GPS Telemetry Data Provide Insights on Winter Habitat Selection of European Roe Deer. - Forests 5: 1374-1390.

Fahrig, L. and Rytwinski, T. 2009. Effects of Roads on Animal Abundance: an Empirical Review and Synthesis. - Ecology and Society 14: 21

Fieberg, J., et al. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2233-2244.

Forester, J. D., et al. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. - Ecology 90: 3554-3565.

Fortin, D., et al. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. - Ecology 86: 1320-1330.

Fox, J. 2003. Effect Displays in R for Generalised Linear Models. - Journal of Statistical Software 8: 1-27.

George, S. L. and Crooks, K. R. 2006. Recreation and large mammal activity in an urban nature reserve. - Biological Conservation 133: 107-117.

Gillies, C. S., et al. 2006. Application of random effects to the study of resource selection by animals. - Journal of Animal Ecology 75: 887-898.

Heurich, M., et al. 2014. Activity Patterns of Eurasian Lynx Are Modulated by Light Regime and Individual Traits over a Wide Latitudinal Range. - Plos One 9: e114143.

Hijmans, R. J. 2015. raster: Geographic Data Analysis and Modeling. - In: R package version 2.3-40.

Hurford, A. 2009. GPS Measurement Error Gives Rise to Spurious 180 degrees Turning Angles and Strong Directional Biases in Animal Movement Data. - Plos One 4: e5632.

Indermaur, L., et al. 2009. Differential resource selection within shared habitat types across spatial scales in sympatric toads. - Ecology 90: 3430-3444.

Jobin, A., et al. 2000. Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. - Acta Theriologica 45: 243-252.

Johnson, C. J., et al. 2002. Movement parameters of ungulates and scale-specific responses to the environment. - Journal of Animal Ecology 71: 225-235.

Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. - Ecology 61: 65-71.

Kaczensky, P., et al. 2012. Status, management and distribution of large carnivores –bear, lynx, wolf and wolverine –in Europe. - In: U. S. L. C. I. f. Europe (ed).

Marshall, E. J. R. and Moonen, A. C. 2002. Field margins in northern Europe: their functions and interactions with agriculture. - Agriculture Ecosystems & Environment 89: 5-21.

Molinari-Jobin, A., et al. 2002. Significance of lynx Lynx lynx predation for roe deer Capreolus capreolus and chamois Rupicapra rupicapra mortality in the Swiss Jura Mountains. - Wildlife Biology 8: 109-115.

Molinari-Jobin, A., et al. 2007. Variation in diet, prey selectivity and home-range size of Eurasian lynx Lynx lynx in Switzerland. - Wildlife Biology 13: 393-405.

Mysterud, A. and Ims, R. A. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. - Ecology 79: 1435-1441.

Newey, W. K. and West, K. D. 1987. A simpel, positive, semidefinite, heteroscedasticity and autocorrelation consistent covariance matrix. - Econometrica 55: 703-708.

Northrup, J. M., et al. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. - Ecology 94: 1456-1463.

Ordiz, A., et al. 2012. Do bears know they are being hunted? - Biological Conservation 152: 21-28.

Oriol-Cotteril, A., et al. 2015. Landscapes of coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. - Oikos 124: 1263-1273.

Pau, G., et al. 2010. EBImage-an R package for image processing with applications to cellular phenotypes. - Bioinformatics 26: 979-981.

Pesenti, E. and Zimmermann, F. 2013. Density estimations of the Eurasian lynx (Lynx lynx) in the Swiss Alps. - Journal of Mammalogy 94: 73-81.

Petrunenko, Y. K., et al. 2016. Spatial variation in the density and vulnerability of preferred prey in the landscape shape patterns of Amur tiger habitat use. - Oikos 125: 66-75.

Plank, M. 2013. Habitat modelling of alpine ibex - Capra ibex - in the Swiss National Park and the National Park Hohe Tauern - A comparison. – Master thesis.

Podgorski, T., et al. 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. - Acta Theriologica 53: 97-110.

Quinn, G. P. and Keough, M. J. 2002. Experimental design and data analysis for biologists. - Experimental design and data analysis for biologists. Cambridge University Press.

Rioux, S., et al. 2013. Avian mortalities due to transmission line collisions: a review of current estimates and field methods with an emphasis on applications to the Canadian electric network. - Avian Conservation and Ecology 8: 7.

Ripple, W.J., et al. 2014. Status and Ecological effects of the world's largest carnivores. – Science 343: 1241484.

Roever, C. L., et al. 2014. The pitfalls of ignoring behaviour when quantifying habitat selection. - Diversity and Distributions 20: 322-333.

Ryser, A., et al. 2005. A remote-controlled teleinjection system for the low-stress capture of large mammals. - Wildlife Society Bulletin 33: 721-730.

Schmidt, K. 1999. Variation in daily activity of the free-living Eurasian lynx (Lynx lynx) in Bialowieza Primeval Forest, Poland. - Journal of Zoology 249: 417-425.

Schmidt-Posthaus, H., et al. 2002. Causes of mortality in reintroduced Eurasian lynx in Switzerland. - Journal of Wildlife Diseases 38: 84-92.

Sibly, R. M., et al. 1990. Splitting behavior into bouts. - Animal Behaviour 39: 63-69.

Sih, A., et al. 2011. Evolution and behavioural responses to human-induced rapid environmental change. - Evolutionary Applications 4: 367-387.

Sunde, P., et al. 1998. Tolerance to humans of resting lynxes Lynx lynx in a hunted population. - Wildlife Biology 4: 177-183.

Sunde, P., et al. 2000. Foraging of lynxes in a managed boreal-alpine environment. - Ecography 23: 291-298.

Thurfjell, H., et al. 2014. Applications of step-selection functions in ecology and conservation. - Movement ecology 2: 4.

Treves, A. and Karanth, K. U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. - Conservation Biology 17: 1491-1499.

Vandyke, F. G., et al. 1986. Reactions of mountain lions to logging and human activity. - Journal of Wildlife Management 50: 95-102.

Warton, D. and Aarts, G. 2013. Advancing our thinking in presence-only and used-available analysis. - Journal of Animal Ecology 82: 1125-1134.

Wiens, T. S., et al. 2008. Three way k-fold cross-validation of resource selection functions. - Ecological Modelling 212: 244-255.

Wilmers, C. C., et al. 2013. Scale Dependent Behavioral Responses to Human Development by a Large Predator, the Puma. - Plos One 8: e60590.

Zahn, A. 1999. Reproductive success, colony size and roost temperature in attic-dwelling bat Myotis myotis. - Journal of Zoology 247: 275-280.

Zeileis, A. 2006. Object-oriented computation of sandwich estimators. - Journal of Statistical Software 16: 1-16.

Zimmermann, F. and Breitenmoser, U. 2002. A distribution model for the Eurasian lynx (Lynx lynx) in the Jura Mountains, Switzerland. - Predicting Species Occurrences: Issues of Accuracy and Scale 653-659.

Zimmermann, F., et al. 2012. Abundanz und Dichte des Luchses in den Nordwestalpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2011/12. - In: KORA, Raubtierökologie und Wildtiermanagement.

Zuur, A. F., et al. 2009. Mixed Effects Models and Extensions in Ecology with R. - Mixed Effects Models and Extensions in Ecology with R. Springer, NY.

Supporting Information Appendix 1

Broken stick model: Explanation for finding the exact break point

Johnson et al. (2002) used non-linear curve fitting for identifying the exact location of the break point (Figure A1 a). However, we identified the movement rate separating the two processes using a simpler maximization routine. First we fitted two linear models for all possible break points and then maximized the combined R^2 of the two models (sum of the sum of squares for the two regression parameters divided by the sum of the total sum of squares of the two models) to find the separation that explained most of the variation in the data. In a next step we tested the best two-process model against a one process model using an F-test. Finally we calculated the optimal speed threshold for separating the two models while minimizing at the same time the number of falsely assigned steps (Sibly et al. 1990, eq. 5).

The average movement rate was dependent on the fix interval. For longer fix intervals the estimated movement speed between locations decreased due to increasing uncertainty in the true movement path for longer step lengths (Figure A1 b; Johnson 2002). As a consequence, the ratio of large scale to small scale movements also decreased with increasing fix interval. To correct for this we calculated more than one break point for different fix intervals. However, inspection of the data revealed that it was only necessary to separate 1 hour intervals from longer intervals. Therefore we estimated two separate broken stick models, one for 1 hour fix intervals and one for the longer fix intervals combined. Subsequently we performed a χ^2-test to confirm similarity in the ratio of fast to slow movements between three fix interval categories (see section in the main text on SSF for fix interval categories).

Estimation of relative importance

We tested the importance of the different model predictors as described in Ewald et al. (2014) by first randomizing each predictor variable in turn and then building models including the permutated predictor. In the end the Pearson correlations between the predictions of the true model and the model with the permutated variable was calculated. Lower correlation values indicate greater importance. We inferred relative importance by subtracting each correlation coefficient from 1 and then scaled the results by dividing each by the sum of all those differences (Table A1). For assessing the overall importance for the core habitat variables we performed the rescaling after summing over all predictors including the particular variable of interest (spatial and temporal interactions included; table 4 in the main text). However, we want to caution here, that this approach does not take collinearities between predictors into account and hence is not an exact measure for relative importance in the model.

Table A1: Table with relative importance for all predictors for the two behaviors (long distance and short-distance movements) at two scales (home range scale and patch scale). HR: Home range, HT: habitat type; ytsin, ytcos, ytsin2, ytcos2: year harmonics; tsin, tcos, tsin2, tcos2: time harmonics, rel. imp.: relative importance.

	Patch scale		HR scale	
	Long distance rel. imp.	Short distance rel. imp.	Long distance rel. imp.	Short distance rel. imp.
Habitat type	0.193	0.056	0.168	0.292
House density	0.038	0.000	0.110	0.113
Edge distance	0.002	0.007	0.037	0.045
Road distance	0.048	0.098	0.008	0.025
Southern exp	0.045	0.000	0.051	0.099
Slope	0.015	0.000	0.062	0.130
Slope sq	0.019	0.000	0.026	0.022
Altitude	0.072	0.279	0.080	0.017
Altitude sq	0.041	0.006	0.029	0.048
HT:edge_distance	0.091	0.337	0.015	0.000
House:Road	0.008	0.033	0.005	0.007
Altitude:ytsin	0.040	0.006	0.042	0.003
Altitude:ytcos	0.109	0.002	0.077	0.060
Altitude:ytsin2	0.069	0.035	0.103	0.061
Altitude:ytcos2	0.003	0.012	0.010	0.003
cover_tsin	0.005	0.006	0.007	0.000
Cover:tcos	0.027	0.000	0.022	0.003
Cover:tsin2	0.004	0.000	0.001	0.000
Cover:tcos2	0.000	0.002	0.000	0.000
Slope:tsin	0.016	0.001	0.009	0.000
Slope:tcos	0.034	0.002	0.037	0.014
Slope:tsin2	0.001	0.000	0.002	0.001
Slope:tcos2	0.001	0.000	0.000	0.001
AspectS:ytsin	0.043	0.000	0.030	0.006
AspectS:ytcos	0.034	0.000	0.016	0.028
AspectS:ytsin2	0.004	0.001	0.002	0.000
AspectS:ytcos2	0.001	0.001	0.000	0.005
Road_dist:tsin	0.001	0.029	0.000	0.000
Road_dist:tcos	0.001	0.003	0.000	0.001
Road_dist:tsin2	0.002	0.071	0.001	0.001

Road_dist:tcos2	0.000	0.004	0.000	0.000
House_density:tsin	0.011	0.002	0.009	0.001
House_density:tcos	0.021	0.006	0.044	0.006
House_density:tsin2	0.000	0.002	0.000	0.006
House_density:tcos2	0.001	0.000	0.000	0.000

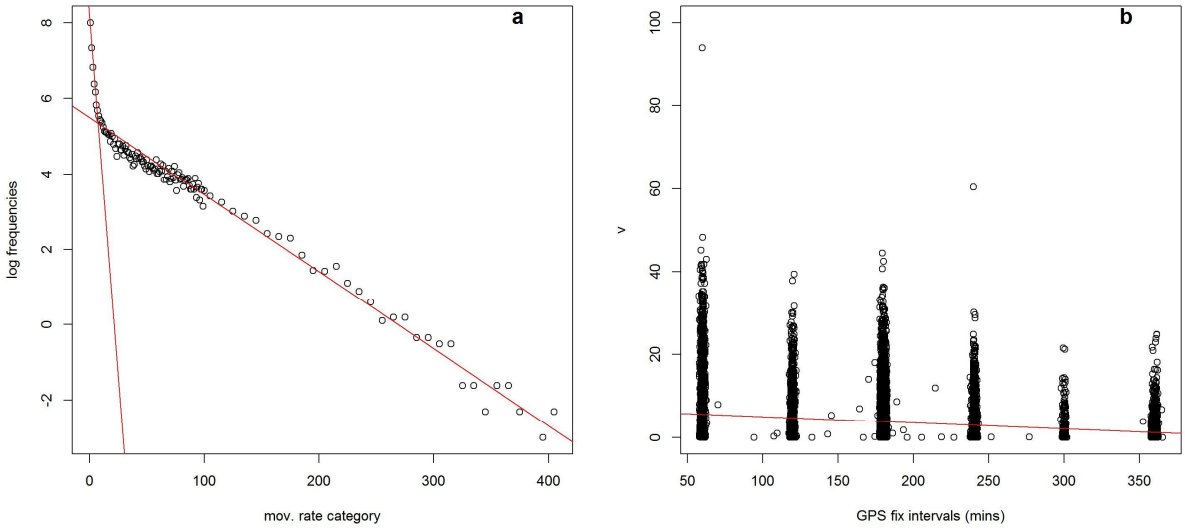

Figure A1: a) Broken stick model for longer fix intervals (3-6h). The log-frequencies of steps in each movement rate category are plotted against the movement rate categories. The two red lines indicate the two best linear model fits for the slow and fast movement process respectively. b) Dependency of movement rate on GPS fix interval. The red line indicates a linear model fit to the data.

References

Ewald, M., et al. 2014. LiDAR Remote Sensing of Forest Structure and GPS Telemetry Data Provide Insights on Winter Habitat Selection of European Roe Deer. - Forests 5: 1374-1390.

Johnson, C. J., et al. 2002. Movement parameters of ungulates and scale-specific responses to the environment. - Journal of Animal Ecology 71: 225-235.

Sibly, R. M., et al. 1990. Splitting behavior into bouts. - Animal Behaviour 39: 63-69.

Chapter 2
Caught in the crossfire of two predators – Hunting-mediated predator facilitation results in superadditive mortality of European roe deer by Eurasian lynx

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Abstract

Predator-prey theory predicts that in the presence of multiple types of predators using common prey, predator facilitation may result as a consequence of contrasting prey defense mechanisms, where reducing the risk from one predator increases the risk from the other. While predator facilitation is well established in natural predator-prey systems, little attention has been payed to situations where human hunters compete with natural predators for the same prey. Here we investigate hunting-mediated predator facilitation in a hunter-predator-prey system. We found that hunter avoidance by roe deer (*Capreolus capreolus*) exposed them to increased predation risk by Eurasian lynx (*Lynx lynx*). Lynx responded by increasing their hunting effort and killing more deer providing strong evidence for superadditive hunting mortality. Our results highlight that human hunters play an important ecological role as top-predators in multi-predator prey systems and affect species interactions at lower trophic levels.

Keywords: habitat selection, prey defense, risk enhancement, step selection, top predator, trophic interactions

Introduction

The risk of predation is one of the key factors shaping animal space use patterns as prey species often have to tradeoff between finding enough food and being eaten (McNamara&Houston 1987, Lima&Dill 1990). Many prey species are eaten by more than one type of predator, resulting in a combination of threats that form a risk landscape through which animals have to move in order to acquire resources and reproduce (Sih et al. 1998).

In the presence of more than one predator, this risk landscape becomes more complex because the effectiveness of a predator to kill its prey depends on the predator-specific hunting mode and the environmental context (Sih et al. 1998). For instance, an ambush predator may rely on cover for effectively catching its prey whereas an aerial predator will only be successful in open habitat. In this example it is easy to see that avoiding one predator (predator-specific prey defense) may increase the risk of being killed by the other. On the other hand, prey can also reduce predation risk from both predators using non-specific prey defenses, for example by reducing general activity, which reduces the overall chance of detection (Lima&Dill 1990). However, such reduced activity may come at the cost of reduced resource acquisition. The phenomenon where the presence of one predator positively affects the hunting success of a second predator via a behavioral response of the prey is called predator facilitation (Charnov 1976). Even though there are many examples of predator facilitation from various systems in different taxonomic groups (e.g. Kotler et al. 1992, Fraser et al. 2004, Cresswell et al. 2013), remarkably little is known about how behavioral changes in game species in response to human hunting may affect their susceptibility to natural predators.

Not only prey adapt their antipredator behavior in the presence of multiple predators. The activity and hunting strategy of predators themselves may depend on whether other predators feeding on the same prey co-occur or not (Matsuda et al. 1993). In this context, Embar et al. (2014) showed experimentally that vipers and owls, both predators of gerbils, adjust their hunting depending on the presence of the other predator. By doing so both predators may be able to improve their own hunting success.

Hunting-mediated predator facilitation may have unexpected implications for the conservation of harvested species, for example if it results in superadditive mortality. Superadditive mortality may occur when harvesting causes additional natural mortality due to suboptimal timing of the hunting season (e.g. in spring after winter mortality has occurred, see Kokko 2001), crippling losses, or when hunting disrupts the social structure of a population (Kokko 2001, Vucetich et al. 2005, Sandercock et al. 2011). Alternatively superadditive mortality may result from a reduction in survival and reproduction through increased stress and lost feeding opportunities as has been shown for natural predator-prey systems (reviewed in Peckarsky et al. 2008). However, super-additive mortality from hunting due to predator

facilitation has rarely been discussed, despite the frequent presence of natural predators in harvested populations (e.g. Brodie et al. 2013, Melis et al. 2013).

In this study, we ask how European roe deer (*Capreolus capreolus*) tradeoff between the risk of being hunted and the risk of being killed by a natural predator, the Eurasian lynx (*Lynx lynx*). Roe deer are the main prey of lynx in most areas where these species co-occur and they are heavily hunted in many parts of Europe (Danilkin & Hewison 1996). Lynx predation alone or in combination with hunting can have considerable effects on roe deer population dynamics depending on the environmental context (Nilsen et al. 2009, Melis 2012). Various studies have shown that roe deer adjust vigilance behavior and habitat selection to both human hunting (Benhaiem 2008, Sönnichsen 2013, Grignolio 2011, Bonnot 2013, Padie 2015) and lynx presence (Eccard 2015, Wikenros 2015). Hunters and Eurasian lynx show contrasting patterns of habitat selection, with hunting risk being highest in open areas and lynx predation risk being highest in habitats with dense understory cover (Norum et al. 2015). The main aim of our study was to quantify the resulting behavioral tradeoffs in predator avoidance and their consequences for deer mortality patterns.

For the following analyses we used 148,125 steps from 60 deer and 18,910 steps from 13 lynx in combination with a large dataset of 13,115 deer mortality causes from over 20 years provided by the local hunting authorities. These two independent sets of data allowed us to consider four questions: (1) Do roe deer exhibit hunting-specific risk avoidance at the expense of being exposed to increased levels of other predation risks? (2) Do roe deer adjust activity patterns during the hunting season as a form of non-specific predator avoidance? (3) Do lynx increase their hunting effort in response to a change in roe deer availability or vulnerability? (4) Do changes in risk avoidance and activity patterns during the hunting season result in super-additive mortality due to predator facilitation?

Our approach sheds light on the ecological role of human hunters as top-predators in multi-predator prey systems and links the behavioral mechanisms that lead to predator facilitation with their ultimate consequences.

Methods

Study area and hunting regime

This study was conducted in the Northwestern Swiss Alps (NWSA). The study area covered roughly 1500km^2 (center coordinates 46.559905 N, 7.513052 E) and ranged in altitude between 600m and 3500m a.s.l. The region is populated by humans (33 inhabitants/km^2) with most human settlements situated at the valley bottoms. The hunting season on chamois *(Rupicapra rupicapra*) and red deer (*Cervus elaphus*) lasts all ofSeptember, whereas roe deer hunting is restricted between October 1 and November 15. For the purpose of this study, we considered the hunting period for all three ungulate species to be relevant, since the entire 10 week period is characterized by an increased frequency of cars and people patrolling in remote places, and previous studies have shown that hunting activities can affect non-target species (e.g. Grignolio 2011). Hunting is allowed between sunrise and sunset. In our study area, roe deer are shot almost exclusively in the open using a sit-and-wait tactic. Hunting with dogs is rare in our study area (B. Gehr pers. Obs.) and therefore can be neglected for the purpose of our study. Lynx density in the region was estimated at 2.05 independent lynx/100 km^2 from a camera-trapping census in winter 2013/14 (Zimmermann et al. 2014). The lynx in this region prey mainly upon roe deer and chamois (Molinari-Jobin et al. 2007). Hence, hunting and lynx predation are the main causes of mortality for roe deer in the area (Breitenmoser&Breitenmoser 2008).

Available data and data preparation

Movement data

Between November 2011 and April 2013 we captured roe deer (n=60) using drive nets or box traps and equipped them with GPS collars (e-obs GmbH, Gruenwald, Germany) recording locations every 30 minutes (n=1,351,368 locations). Because mean GPS error (27m) was large with respect to the mean step length of 54m (Visscher 2005) we rarefied the data to 2h fix intervals resulting in a data set with 302’633 deer locations (mean step length=123m). Simultaneously, 13 lynx were GPS-collared in our study area, yielding 18’910 GPS locations of lynx during the same period. Capture protocol and data collection for lynx are described elsewhere (Gehr et al. in review).

Mortality data

The cantonal hunting authorities provided us with an independent data set of reported cause-specific mortalities of 13,832 roe deer in the study area (based on reports from game wardens and researchers) between 1990 and 2014 (n=13,115; data for the year 2013 were excluded as mortality data for most mortality causes deviated considerably from all other years for unknown

reasons). For the purpose of our study, we extracted the data on natural mortality (disease and starvation; 4% of all mortality records) and lynx predation (5%) from this data set.

Separating movement data of lynx and deer into active and passive states

Roe deer

Because most deer are shot in the open while actively feeding, we restricted the analysis of risk avoidance of deer to their active phases. For this reason we separated location data from all deer into active and passive states based on tri-axial accelerometer data recorded for each deer (see Appendix S1 in Supporting Information).

Lynx

We used a previously developed broken stick model (Gehr et al. in review) to separate lynx steps into short and long distance movements based on movement speed (Appendix S1). Data processing and modelling followed Gehr et al. (in review). For the purpose of this study, we considered long distance movements of lynx to represent an active state, and short distance movements a passive state.

Statistical analysis of question 1: Tradeoffs in risk avoidance between humans and lynx

Defining variables for modelling risk avoidance

For the first question it was our main interest to investigate how deer would tradeoff between the risk of being hunted and the risk of being killed by a lynx while being active. The variables we used to model seasonal variation in risk avoidance and habitat selection of roe deer were defined as follows: As most deer are shot in the open (see above), we used open habitat and forest as a proxy for high and low hunting risk. We used a previously developed habitat selection model for lynx during long distance movements as a proxy for predation risk (Gehr et al. in review and Appendix S1). In addition we accounted for environmental variables that are known to be important for roe deer habitat selection (table 1). The justification to include each of the variables in table 1 is as follows: Roe deer occur at high densities in fragmented cultivated land where they are closely associated with forest edges at the interface of open habitat and forest (Danilkin 1996). Open habitats provide rich feeding opportunities for deer but are associated with increased hunting risk whereas forests provide refuge (Padie et al. 2015). Therefore, open habitat was included as a dummy variable with 1=open (high hunting risk), and 0=forest (low hunting risk). We further included distance to the closest forest edge to account for the fact that deer may evaluate risk in the open depending on the distance to cover. We included house density as well as proximity to roads as a proxy for human disturbance (Zimmermann et al. 2002). Furthermore, we included altitude and slope, since altitude correlates with climate variables whereas steep slopes have been associated with low human activity in previous studies and may

serve as a refuge for roe deer (Zimmermann et al. 2002, Basille et al. 2009, but also see Lone et al. 2014). For both altitude and slope a quadratic term was included to allow for non-linear dependencies between selection and those covariates. Finally southern exposed slopes (dummy variable with 1=southern exposed slope and 0=all other directions) may be preferred by ungulates during winter because this is where snow cover first disappears (e.g. Plank 2013).

Disentangling seasonal from hunting effects

Over the course of the study 13 deer were hunted. However, all deer included in this study were exposed to hunting pressure, which precluded a comparison of hunted with non-hunted individuals. Instead, we compared the observed data during the hunting season with habitat use during that time predicted based on the data from the rest of the year. To do so, we built two separate habitat selection models using two nested datasets, the full dataset which included all location data over the entire year (the hunting model), and a reduced data set in which we excluded the 10 week hunting period from the data (no-hunting model). In the second model, we interpolated roe deer habitat use during the missing hunting period from the remaining data. This allowed us to compare the behavior during the hunting period to that expected based on the non-hunting period.

We modelled seasonal variation of risk avoidance behavior on a continuous time scale following the approach used in Forester et al. (2009), by including interaction terms between open habitat and predation risk and four harmonics of day of year (DOY): $s_{1DOY}=\sin(2\pi t/365)$, $s_{2DOY}=\sin(4\pi t/365)$, $c_{1DOY}=\cos(2\pi t/365)$, $c_{2DOY}=\cos(4\pi t/365)$). In addition we included DOY interactions for altitude and southern exposed slopes as we expected habitat selection of these variables to vary over seasons. Because human activity as well as lynx activity also differ between day and night, we further accounted for diurnal fluctuations of deer risk avoidance and habitat selection in our models by including additional interactions for open habitat and lynx predation risk as well as building density, distance to road, distance to forest edges and slope with two harmonics of time of day (TOD: $s_{1TOD}=\sin(2\pi t/24)$, $s_{2TOD}=\sin(4\pi t/24)$). This accounted for diurnal fluctuations averaged over the entire year (Forester et al. 2009).

All continuous covariates were standardized (mean of 0 and SD of 1). We used variance inflation factors (VIF) to test for multicollinearities between all model covariates. Lynx predation risk was associated with the highest variance inflation factor (VIF=5.61). Most of this inflation was caused by the interactions between lynx predation risk and DOY and TOD (when excluding these, VIF dropped to 2.65). However, perhaps in part because of the very large sample sizes, there was no indication that the models were sensitive to the inclusion/exclusion of single predictor variables, hence this multicollinearity did not seem to be an issue in our models (Zuur et al. 2009). For all analyses we standardized time of day to Coordinated Universal Time (UTC).

Analysis of risk avoidance using step selection functions

To model deer tradeoffs in risk avoidance between humans and lynx we built step selection functions (SSF; (Fortin et al. 2005). First animal paths were broken down into successive steps characterized by the step length (the straight-line segment between two successive locations) and the turning angle (the angle between the previous and the current step). Each step was then assigned habitat variables and predation risk found at the end of the step. We restricted the analysis to steps that were assigned to an active state (see above). Thus, we used 148,525 active steps for the full data model and 122,675 active steps for the reduced no-hunting model. Each realized step of the final datasets was paired with 10 alternative random steps which shared the same origin but had different end points. Random step lengths and turning angles were drawn in pairs from the empirical distributions in the data (Thurfjell 2014). In the end we modelled risk avoidance and habitat selection using conditional logistic regression for case-control data with choice sets of 1 case and 10 control locations. To account for characteristics of animal movement we included step length as a predictor in the regression analysis (Forester 2009). Conditional logistic regression does not allow to fit main effects for predictors that are constant within choice sets, which was the case for DOY and TOD (Allison 1991, Fortin et al. 2009a). Consequently we fitted all temporal predictors only as interaction terms (table 1). To account for serial autocorrelation in the data we calculated robust standard errors as described in Forester et al. (2009, Appendix C; see Appendix S1 in Supporting Information). Analyses of autocorrelation for the deviance residuals of the model indicated that autocorrelation could be neglected for lags beyond 9 steps (18 hours).

To assess differences between the full-data hunting model and the reduced no-hunting model, we calculated 95% effect displays for the predicted values under the different models using the robust covariance matrix as described in Appendix S1 (Forester et al. 2009, Fox 2003). We considered differences to be significant when effect displays for the models did not overlap.

We tested the relative importance of the different model predictors using a resampling procedure as described in Ewald et al. 2014 (see Appendix S1). Finally we performed k-fold cross-validation for a case-control design as described in Fortin et al. (2009b) to assess the goodness of fit of our models (see Appendix S1). Following Fortin et al. (2009b), we repeated the cross-validation for a null model where we assumed a completely random pattern of habitat selection.

Statistical analyses of questions 2&3: Activity models for roe deer and lynx

In questions 2 and 3 we looked at the effect of hunting on the activity of roe deer and lynx. For the deer we were interested in how hunting and predation risk affect the proportion of time animals spend active while accounting for the same environmental covariates as in the SSF models. Similarly, for the lynx we used the same habitat covariates for the activity model as for the lynx habitat model (table 1; described in Gehr et al. in review). We modeled the temporal

fluctuations in the proportion of time deer and lynx spent active using a logistic regression approach modelling the probability of a step being assigned to an active phase (P(active=1); table 1). To disentangle the seasonal from hunting effects we applied the same approach as for the SSF models by fitting and comparing two nested models; one with the full data set (hunting model) and a reduced model where the hunting data were excluded (non-hunting model; see above). Furthermore we restricted the analysis to the time between the beginning of astronomical twilight in the morning (sun angle less than 18 degrees below the horizon) and the end of astronomical twilight in the evening (sun angle larger than 18 degrees below the horizon). We did this because we expected a tradeoff between contrasting predation risks to show while both predators are active (hunters and lynx). In the end, we used 205,596 deer locations and 11,469 lynx locations for the activity analyses. To capture temporal effects, we included interactions of covariates with harmonics of TOD and DOY in the same way as we did for the SSF models. However, for the logit models we also included main effects for the temporal predictors. Analyses of autocorrelation for the deviance residuals of the logit models indicated that autocorrelation could be neglected for lags beyond 2 steps (4 hours) for deer and beyond 8 lags (24 hours) for lynx. We then accounted for serial autocorrelation in the data using the NeweyWest function in the sandwich package in R (Newey and West 1987). We performed model comparisons as described for the SSF by plotting 95% effect displays based on the robust covariance matrix.

Statistical analysis of question 4: Seasonal variation of lynx predation and natural mortality

In question 4 we were interested whether lynx predation was affected by the hunting season. The structure of our data precluded a direct test in the form of a competing risk analysis (Lunn&McNeil 1995). We therefore opted for a more indirect approach: to visualize the seasonal variation in occurrence of lynx predation and natural mortality as a function of day of year (DOY). We used a moving window average with a window size of 31 days to get a smoothed function of the number of lynx kills over the course of a year. In the end we then calculated the estimated percental increase in lynx predation due to hunting as described in Appendix S1. The frequencies of the different mortality causes in the records do not represent the true frequencies of occurrence, as the detection probability for the different causes is likely to vary considerably. However, we assumed that the detection probabilities *within* mortality causes remain roughly constant over the course of a year and therefore reflect true seasonal variation (see Discussion on possible shortcomings of this assumption).

Results

Question 1: Tradeoffs in risk avoidance between humans and lynx

Comparison between the hunting and the no-hunting model revealed clear evidence that roe deer tradeoff risk avoidance during the hunting season. During the 10 week hunting period roe deer spent less time in open habitat where hunting risk is high at the expense of being exposed to higher lynx predation risk. On average the hunting model predicted 24% lower selection of cover and 26% higher selection of predation risk during the hunting season than the no hunting model (Figure 1). In contrast, for altitude and southern exposed slopes there was no difference in selection/avoidance between the hunting and no-hunting models (table S2 and Figure S2 in Appendix S1). In general, avoidance of open habitat as well as lynx predation risk showed strong seasonal variation with strongest avoidance in winter and summer and less avoidance during spring and fall (Figure 1, table S1 in Appendix S1). In addition, avoidance of lynx predation risk was much stronger during winter than in summer.

Cross-validation indicated that both models predicted roe deer habitat use well (mean Spearman rank correlations r_{s_Hunt}=0.997, $r_{s\_No\text{-}hunt}$=0.995) and were clearly different from the null model of random space use (table 2). Inspection of the relative importance of the different covariates in the two models showed that open habitat, distance to edge, and altitude were the most important predictors for deer habitat use (table 2). The relative importance of predation risk as a model predictor was very different between the hunting and no-hunting model (9% in the hunting model and 17% in the no-hunting model). For all other predictors, the relative importance was very similar between the two models (table 2).

Question 2: Activity model for roe deer

The comparison of the hunting and no-hunting logit model showed reduced activity of roe deer in the open between dawn and dusk during the hunting season. On average deer activity for the hunting model was predicted to be 11% lower during the hunting season than for the no hunting model (Figure 2, table S3 in Appendix S1). In contrast, there was no difference in activity between the hunting and no-hunting period inside the forest, where hunting risk is low in our study area. In general roe deer were less active in the forest than in the open over the course of the year, however, this difference almost disappeared during the summer months (Figure 2).

Question 3: Activity model for lynx

In general lynx were more active when in the open than when in the forest. In contrast to the deer however, lynx increased their activity inside the forest during the hunting season between dawn and dusk whereas activity did not change significantly in the open. Lynx activity during the

hunting season for the hunting model was on average 44% higher than for the no hunting model (Figure 2, table S4 in Appendix S1). (Figure 2).

Question 4: Seasonal variation of lynx predation and natural mortality

Most lynx kills in the study area were found in the second half of winter. In addition we observed a pronounced increase in the occurrence of reported lynx kills during the hunting season and a second but smaller peak of lynx kills in August during the breeding season of roe deer (Figure 3). The increase in lynx predation attributable to hunting based on Figure 3 was roughly 21%. In contrast, there was no increasing occurrence of natural mortality during the hunting season. Most natural mortality occurred in late winter and during the fawning season.

Table 1 Model specifications for risk avoidance (step selection function - SSF) and activity patterns (LOGIT model) in roe deer and lynx. A 1 denotes inclusion of a particular model parameter. DOY: day of year. TOD: Time of day. HT: Habitat type. RSF: The resource selection function for the lynx is described in Gehr et al. (in review) and Appendix S1.

	Roe deer		**Lynx**	
	SSF	LOGIT	RSF*	LOGIT
Habitat variables				
Habitat type (HT)	1	1	1	1
Edge distance	1	1	1	1
Altitude	1	1	1	1
Altitude sq	1	1	1	1
Slope	1	1	1	1
Slope sq	1	1	1	1
House density	1	1	1	1
Road distance	1	1	1	1
Southern exposition	1	1	1	1
Time variables				
DOY	-	1	-	1
TOD	-	1	-	1
Spatial interactions				
HT:edge distance	-	-	1	1
House:Road	-	-	1	1
Temporal interactions				
HT:TOD	1	1	1	1
HT:DOY	1	1	-	-
PR:TOD	1	1	-	-
PR:DOY	1	1	-	-
Edge_dist:TOD	1	1	-	-
Slope:TOD	1	1	1	1
House_density:TOD	1	1	1	1
Road_dist:TOD	1	1	1	1
Altitude:DOY	1	1	1	1
Southern exp:DOY	1	1	1	1

Table 2 Relative importance of the different habitat variables in the SSF models (summed over the main effect and all interaction terms) together with the results for the cross-validation analysis. Cross-validation results represent the mean and range (in parentheses) of the Spearman rank correlations of 100 independent trials for used and random locations as described in Fortin et al. (2009b).

	Hunting model	Non-hunting model
Habitat type	0.22	0.21
Predation risk	0.09	0.16
Edge distance	0.24	0.23
House density	0.05	0.04
Road distance	0.09	0.08
Slope	0.06	0.06
Altitude	0.21	0.18
Southern exposition	0.04	0.04
Sum	1	1

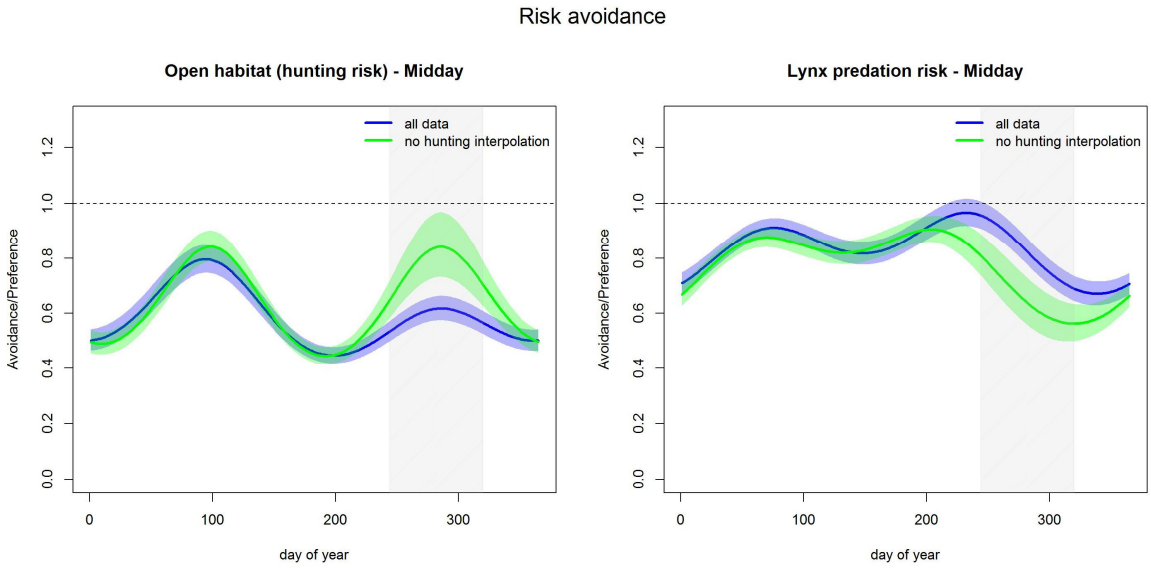

Figure 1 Contrasting risk avoidance in response to hunting (left panel) and lynx predation risk (right panel) shown for midday. Blue curves show the selection/avoidance values (w(x)=exp(coef)) of the step selection function (SSF) in the hunting model whereas green curves indicate selection/avoidance in the non-hunting model. The color shaded areas denote the robust 95% -pointwise confidence intervals for the hunting (blue) and the non-hunting model (green), respectively. To calculate the effect displays, all covariates were set to 0 except for open habitat (left panel) or predation risk (right panel). The shaded area in grey depicts the 10 week hunting period in the fall. The dotted line for w(x)=1 represents no selection/avoidance. Since predation risk is a continuous variable we fixed it at the 75% quantile value for data visualization. Thus the response shown denotes the avoidance of high predation risk (75% quantile) relative to the mean predation risk over the course of the year.

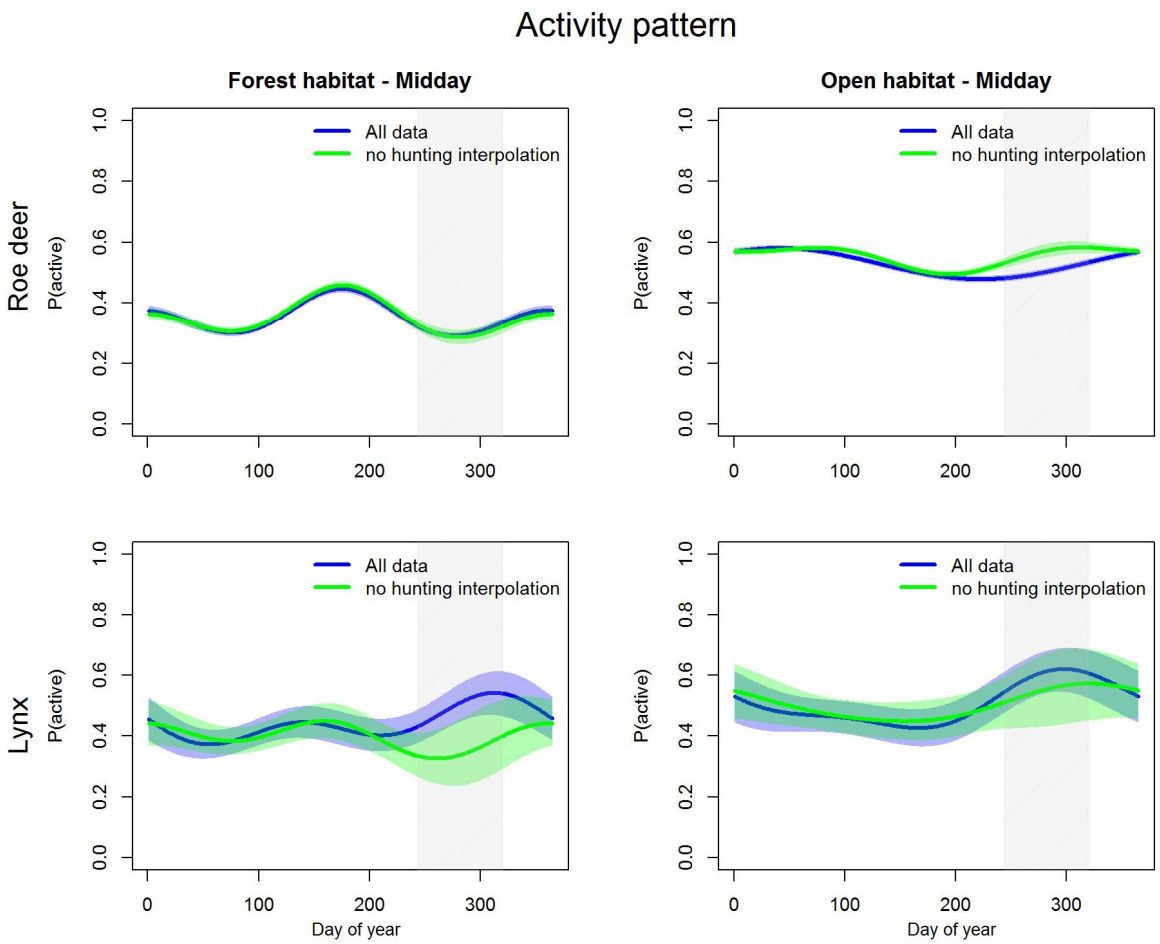

Figure 2 Contrasting activity patterns of roe deer (upper panels) and lynx (lower panels) over the course of the year. The results show the probability of a deer/lynx being active inside the forest (left panels) and in the open (right panels) while setting all other covariates to 0 (continuous predictors were standardized). For the deer models, predation risk was set to the minimum value to show the effect of hunting on deer activity in the absence of predation risk. Blue curves show the activity for the hunting model, green curves for the non-hunting model. The color shaded areas denote the robust 95% -pointwise confidence intervals for the hunting (blue) and the non-hunting model (green). The shaded area in grey depicts the 10 week hunting period in the fall.

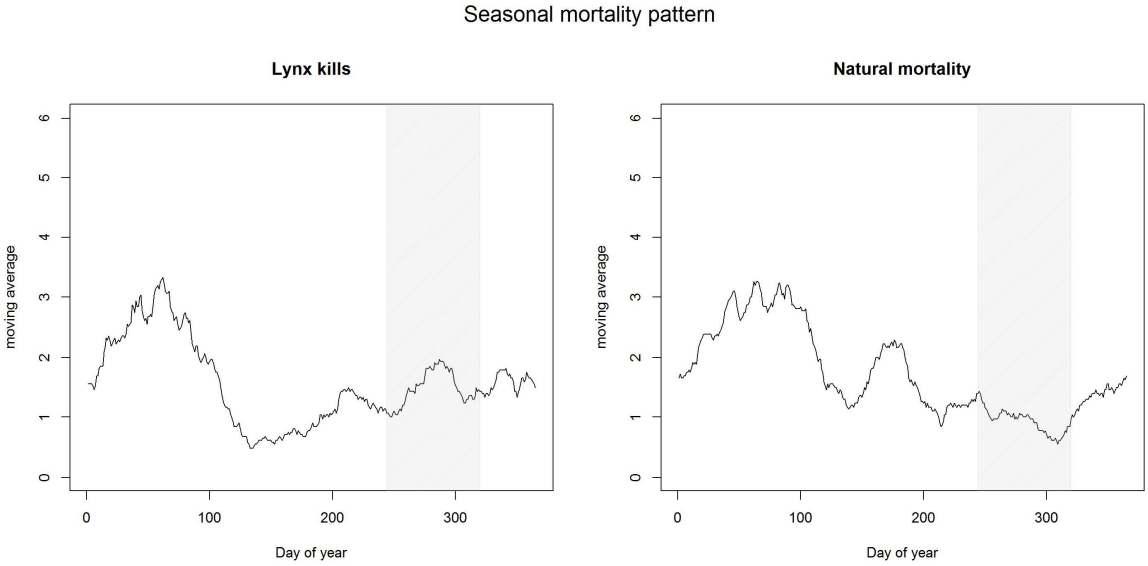

Figure 3 Seasonal mortality patterns for roe deer based on data from lynx kills (left panel) and natural mortalities (right panel). Results show the moving averages over 31 days. The shaded area in grey depicts the 10 week hunting period in the fall.

Discussion

The main aim of our study was to empirically quantify the behavioral tradeoffs of roe deer between hunter avoidance and lynx avoidance, and to ask whether such tradeoffs increases a deer's susceptibility to lynx predation. We found that roe deer avoid areas of high hunting risk during the hunting season at the expense of higher exposure to lynx predation risk, and that lynx increased their activity and hunting success during this time period. We show that hunting can induce predator facilitation through behavioral changes in both predator and prey and there was strong evidence that this resulted in superadditive mortality. Given the frequent occurrence of natural predators in areas of harvested populations we believe this topic merits further investigation in order to verify its generality and quantify its magnitude in other systems. In the following we discuss in detail the four questions we asked in the introduction:

Question 1: Tradeoffs in risk avoidance between humans and lynx

Our results show that a shift in habitat use as a hunting-specific prey defense can lead to increased exposure to a natural predator in a hunter-predator-prey system (Figure 1). Roe deer clearly avoided open habitat, moreso during the hunting season than would be expected from purely seasonal fluctuations in habitat preference. Similar shifts in habitat preference in response to hunting have also been found in other roe deer studies where natural predators were absent or very rare (e.g. Bonnot et al. 2013, Padie et al. 2015). In our study area, however, a natural predator, the lynx, is common. Our results show that in the presence of this natural predator the observed hunting avoidance behavior of roe deer leads to increased exposure to lynx predation risk which ultimately resulted in increased predation rates (see below). These findings are in line with theoretical predictions that predators with different foraging modes (here sit-and-wait in open habitat vs ambush in the forest) will provoke conflicting predator-specific defenses resulting in an overall risk increase for the prey (Sih et al. 1998). The fact that roe deer changed their behavior in response to the hunting season in fall further suggests that they perceived the temporary high hunting pressure as a more imminent risk than the year-round background predation risk from lynx. This supports the view that the distribution of prey in a multi-predator-prey system reflects the attack frequency and success rate of all predators combined (Cresswell & Quinn 2013).

Question 2: Activity model for roe deer

In addition to shifting their preferred habitat, roe deer also reduced their general activity during the hunting season in open habitat, where they are most often shot (Figure 2). Although this effect was clear, it was not very strong (11% activity reduction). It is unclear whether the reduced activity in the open was a result of increased vigilance behavior during active phases or a defense mechanism to avoid being detected by a hunter. Vigilance behavior and activity reduction is

generally considered to be a non-specific prey defense mechanisms directed at any predator (Sih et al. 1998). However, roe deer only reduced their activity in open habitat associated with high hunting risk whereas activity did not change inside the forest where lynx predation risk is high. The deer thereby seemed to respond specifically to the altered risk situation from hunters in the open, whereas in the forest the lynx predation risk level remained unchanged.

Question 3&4: Activity model for lynx and seasonal variation of lynx predation

In addition to the response of the prey to changes in the risk landscape, we also found a behavioral response in the predator. There was strong evidence that lynx increased their activity during the hunting season in the forest but not in open habitat to benefit from the increased prey availability/vulnerability during this short time period (Figure 2). The observed increase in reported lynx kills by more than 20% during the hunting season (Figure 3) supports this interpretation, and links the behavioral shifts in roe deer to increased lynx predation as a result of predator facilitation. In this context, a more direct tests in the form of a competing risk analysis would be able to confirm the true superadditive nature of lynx predation (Lunn&McNeil 1995).

Our study shows that predator facilitation may prompt predators to increase their hunting efforts in their preferred habitat in the presence of other predators that hunt the same prey (Embar et al. 2014). It is difficult to predict the population-level effect of hunting-mediated predator facilitation on lynx and roe deer populations. Lynx have been found to kill roughly one deer per week (Sunde et al. 2000, Molinari-Jobin et al. 2002). The 20 percent increase in lynx kills that we found, implies that each lynx would kill about 2 additional deer due to hunting during the 10 week period in fall. Given the lynx density in the area this would add up to roughly 4 additional deer per 100km^2 (Zimmermann et al. 2014). These numbers don't seem very high even if deer densities were low. However, short-term and long-term effects for both predator and prey may be very different in multi-predator-prey systems (Matsuda et al. 1993). Hunting may positively affect lynx hunting success in the short run through risk enhancement, however, if hunting eventually depresses deer density over time, long-term effects of hunters on both roe deer and lynx may be negative (Sih et al. 1998). In order to better understand potential short-term and long term consequences of hunting-mediated predator facilitation, it will be necessary to quantify mortality rates of roe deer in areas with hunters and lynx present alone or in combination with each other. Only an experimental approach would enable a test of the different trophic interactions between the players in this hunter-predator-prey system. Furthermore such an approach will allow to test directly for superadditive mortality and be able to confirm our finding in this study.

An alternative explanation for the increased kill rate during the hunting season could be that lynx abandon their kills prematurely in response to high hunter disturbance and therefore have to invest more time into searching and killing new prey, as has been found in a study on cougars in California (Smith et al. 2015). However, if this were the case, we would expect lynx to also

increase their activity at night to hunt when human hunters are not active. We had no indication that this was the case (Figure S3 in Appendix S1), nor did we find a decreased activity in the open where hunters are most active. For these reasons, we believe that it is unlikely that the increased activity of lynx during the hunting season is a response to a perceived threat from hunters. Biased reporting of roe deer carcasses due to increased hunter activity during the hunting season also does not seem to explain the higher roe deer predation by lynx (Figure 3a). Such reporting biases are known from bird studies, where band recoveries are used to estimate survival (e.g. Souchay et al. 2014). However, increased detection probabilities during the hunting season should affect natural mortalities just as much as lynx kills. No peak in natural mortality was evident during the hunting season (Figure 3b), making it unlikely that an increased detection probability caused the observed pattern in lynx kills. Instead, the results show the behavioral plasticity of lynx that enable them to capitalize on short-term changes in prey availability or vulnerability.

Conclusions

Our results show, that humans can alter the natural risk landscape of a prey, and induce behavioral changes that result in super-additive mortality through predator facilitation. These findings have important implications for understanding the ecological role of humans as top predators driving lower trophic interactions in natural ecosystems. Furthermore, our study highlights the need for more empirical, detailed studies of harvested populations to determine the generality of our findings. Although we are aware of the difficulties of performing experimental studies in populations harvested by recreational hunters, we strongly recommend an experimental approach to shed light on hunting as an ecological force shaping prey population dynamics.

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References

Allison, P.D. (1991). Logistic regression using the SAS system - Theory and application. Cary, NC: SAS Institute Inc.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R. et al. (2009). What shapes Eurasian lynx distribution in human-dominated landscapes: selecting prey or avoiding people? Ecography, 32, 683-691.

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M. et al. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour, 76, 611-618.

Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. et al. (2013). Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research, 59, 185-193.

Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999). Seasonal compensation of predation and harvesting. Oikos, 87, 419-426.

Breitenmoser, U. & Breitenmoser-Würsten, C. (2008). Der Luchs-Ein Grossraubtier in der Kulturlandschaft. Salm Verlag.

Brodie, J., Johnson, H., Mitchell, M., Zager, P., Proffitt, K., Hebblewhite, M. et al. (2013). Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology, 50, 295-305.

Burnham, K.P. & Anderson, D.R. (1984). Tests of Compensatory Vs Additive Hypotheses of Mortality in Mallards. Ecology, 65, 105-112.

Charnov, E.L., Orians, G.H. & Hyatt, K. (1976). Ecological Implications of Resource Depression. American Naturalist, 110, 247-259.

Cresswell, W. & Quinn, J.L. (2013). Contrasting risks from different predators change the overall nonlethal effects of predation risk. Behavioral Ecology, 24, 871-876.

Danilkin, A. & Hewison, A.J.M. (1996). Chapman and Hall Wildlife Ecology and Behaviour Series: Behavioural ecology of Siberian and European roe deer. Chapman and Hall Wildlife Ecology and Behaviour Series; Behavioural ecology of Siberian and European roe deer, xvi+277p-xvi+277p.

Eccard, J.A., Meißner, J.K. & Heurich, M. (2015). European Roe Deer Increase Vigilance When Faced with Immediate Predation Risk by Eurasian Lynx. Ethology, n/a-n/a.

Eloff, P. & van Niekerk, A. (2008). Temporal patterns of animal-related traffic accidents in the Eastern Cape, South Africa. South African Journal of Wildlife Research, 38, 153-162.

Embar, K., Kotler, B.P. & Mukherjee, S. (2011). Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. Oikos, 120, 1657-1666.

Embar, K., Raveh, A., Hoffmann, I. & Kotler, B.P. (2014). Predator facilitation or interference: a game of vipers and owls. Oecologia, 174, 1301-1309.

Ewald, M., Dupke, C., Heurich, M., Mueller, J. & Reineking, B. (2014). LiDAR Remote Sensing of Forest Structure and GPS Telemetry Data Provide Insights on Winter Habitat Selection of European Roe Deer. Forests, 5, 1374-1390.

Forester, J.D., Im, H.K. & Rathouz, P.J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology, 90, 3554-3565.

Fortin, D. & Fortin, M.-E. (2009). Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. Animal Behaviour, 78, 887-892.

Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. Ecology, 90, 2480-2490.

Fox, J. (2003). Effect Displays in R for Generalised Linear Models. Journal of Statistical Software, 8, 27.

Fraser, D.F., Gilliam, J.F., Akkara, J.T., Albanese, B.W. & Snider, S.B. (2004). Night feeding by guppies under predator release: Effects on growth and daytime courtship. Ecology, 85, 312-319.

Grignolio, S., Merli, E., Bongi, P., Ciuti, S. & Apollonio, M. (2011). Effects of hunting with hounds on a non-target species living on the edge of a protected area. Biological Conservation, 144, 641-649.

Heurich, M., Hilger, A., Kuechenhoff, H., Andren, H., Bufka, L., Krofel, M. et al. (2014). Activity Patterns of Eurasian Lynx Are Modulated by Light Regime and Individual Traits over a Wide Latitudinal Range. Plos One, 9.

Kokko, H. (2001). Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. Wildlife Biology, 7, 141-150.

Koper, N. & Manseau, M. (2009). Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. Journal of Applied Ecology, 46, 590-599.

Kotler, B.P., Blaustein, L. & Brown, J.S. (1992). Predator Facilitation - The Combined Effect Of Snakes And Owls On The Foraging Behavior Of Gerbils. Annales Zoologici Fennici, 29, 199-206.

Lagos, L., Picos, J. & Valero, E. (2012). Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. European Journal of Wildlife Research, 58, 661-668.

Lebreton, J.D. (2005). Dynamical and statistical models for exploited populations. Australian & New Zealand Journal of Statistics, 47, 49-63.

Lima, S.L. & Dill, L.M. (1990). Behavioral Decisions Made under the Risk of Predation - a Review and Prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie, 68, 619-640.

Lunn, M. & McNeil, N. (1995). APPLYING COX REGRESSION TO COMPETING RISKS. Biometrics, 51, 524-532.

Matsuda, H., Abrams, P.A. & Hori, H. (1993). The Effect Of Adaptive Antipredator Behavior On Exploitative Competition And Mutualism Between Predators. Oikos, 68, 549-559.

Mcnamara, J.M. & Houston, A.I. (1987). Starvation and Predation as Factors Limiting Population-Size. Ecology, 68, 1515-1519.

Melis, C., Basille, M., Herfindal, I., Linnell, J.D.C., Odden, J., Gaillard, J.-M. et al. (2010). Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. Ecoscience, 17, 166-174.

Melis, C., Jedrzejewska, B., Apollonio, M., Barton, K.A., Jedrzejewski, W., Linnell, J.D.C. et al. (2009). Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Global Ecology and Biogeography, 18, 724-734.

Mills, L.S. (2006). Conservation of Wildlife Populations: Demography, Genetics and Management. Blackwell Publishing.

Molinari-Jobin, A., Molinari, P., Breitenmoser-Wursten, C. & Breitenmoser, U. (2002). Significance of lynx Lynx lynx predation for roe deer Capreolus capreolus and chamois Rupicapra rupicapra mortality in the Swiss Jura Mountains. Wildlife Biology, 8, 109-115.

Molinari-Jobin, A., Zimmermann, F., Ryser, A., Molinari, P., Haller, H., Breitenmoser-Wursten, C. et al. (2007). Variation in diet, prey selectivity and home-range size of Eurasian lynx Lynx lynx in Switzerland. Wildlife Biology, 13, 393-405.

Newey, W.K. & West, K.D. (1987). A Simple, Positive Semidefinite, Heteroskedasticity And Autocorrelation Consistent Covariance-Matrix. Econometrica, 55, 703-708.

Nilsen, E.B., Gaillard, J.M., Andersen, R., Odden, J., Delorme, D., van Laere, G. et al. (2009). A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. Journal of Animal Ecology, 78, 585-594.

Norum, J.K., Lone, K., Linnell, J.D.C., Odden, J., Loe, L.E. & Mysterud, A. (2015). Landscape of risk to roe deer imposed by lynx and different human hunting tactics. European Journal of Wildlife Research, 61, 831-840.

Padie, S., Morellet, N., Hewison, A.J.M., Martin, J.-L., Bonnot, N., Cargnelutti, B. et al. (2015). Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos, 124, 1536-1546.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B. et al. (2008). Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology, 89, 2416-2425.

Plank, M. (2013). Habitat modelling of alpine ibex - Capra ibex - in the Swiss National Park and the National Park Hohe Tauern - A comparison. In: Institut für Wildbiologie und Jagdwirtschaft. Universität für Bodenkultur, Wien, p. 43.

Proffitt, K.M., Grigg, J.L., Hamlin, K.L. & Garrott, R.A. (2009). Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. Journal of Wildlife Management, 73, 345-356.

Sandercock, B.K., Nilsen, E.B., Broseth, H. & Pedersen, H.C. (2011). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology, 80, 244-258.

Schmidt-Posthaus, H., Breitenmoser-Wursten, C., Posthaus, H., Bacciarini, L. & Breitenmoser, U. (2002). Causes of mortality in reintroduced Eurasian lynx in Switzerland. Journal of Wildlife Diseases, 38, 84-92.

Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution, 13, 350-355.

Smith, J.A., Wang, Y. & Wilmers, C.C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. Proceedings of the Royal Society B-Biological Sciences, 282.

Soennichsen, L., Bokje, M., Marchal, J., Hofer, H., Jedrzejewska, B., Kramer-Schadt, S. et al. (2013). Behavioural Responses of European Roe Deer to Temporal Variation in Predation Risk. Ethology, 119, 233-243.

Souchay, G., Gimenez, O., Gauthier, G. & Pradel, R. (2014). Variations in band reporting rate and implications for kill rate in Greater Snow Geese. Avian Conservation and Ecology, 9, 1-1.

Sunde, P., Kvam, T., Bolstad, J.P. & Bronndal, M. (2000). Foraging of lynxes in a managed boreal-alpine environment. Ecography, 23, 291-298.

Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. Movement ecology, 2, 4-4.

Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005). Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos, 111, 259-270.

Wikenros, C., Kuijper, D.P.J., Behnke, R. & Schmidt, K. (2015). Behavioural responses of ungulates to indirect cues of an ambush predator. Behaviour, 152, 1019-1040.

Zimmermann, F. & Breitenmoser, U. (2002). A distribution model for the Eurasian lynx (Lynx lynx) in the Jura Mountains, Switzerland. Predicting Species Occurrences: Issues of Accuracy and Scale, 653-659.

Zimmermann, F., Foresti, D., Bach, J., Dulex, N., Wuersten-Breitenmoser, C. & Breitenmoser, U. (2014). Abundanz und Dichte des Luchses in den Nordwestalpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2013/14.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). Mixed Effects Models and Extensions in Ecology with R. Mixed Effects Models and Extensions in Ecology with R.

Supporting Information Appendix S1

Separating roe deer steps into active and passive state using tri-axial accelerometer data

We separated location data from all deer into active and passive state based on tri-axial accelerometer data recorded for each deer. We first calculated 5 minutes acceleration averages (measured in millivolts) over all three axes and subsequently applied a running window of size two (averaging over two 5-minutes bursts) over all data for each deer. Then we plotted the moving acceleration averages against time and visually identified a threshold value which clearly separated active from passive phases for all animals (Figure S1). In our data set 10 millivolts clearly separated the data into these two states. Further increasing the threshold did not result in significant changes in activity states. Next we divided these moving averages into active and passive sequences based on the defined threshold value: an active burst started the first time the threshold was exceeded and ended the first time it fell below the threshold again. To avoid short periods of active behavior to be classified as a change in activity state (e.g. scratching while lying down and resting), we set the minimum length of an active phase to be 10 minutes. Again, shortening or prolonging this minimum length did not result in major changes in the duration of the activity bursts. Finally the time of the activity bursts was intersected with the time of the GPS fix to assign each location an activity state.

Separating lynx steps into long distance and short distance movements using a broken-stick model

To separate lynx movements into short-distance and long-distance movements, we applied a broken-stick model based on speed (Sibly et al. 1990, Johnson et al. 2002). A two-process broken-stick model assumes that two Poisson processes generate movement rates. To separate the data into the two processes, we first categorized the movement rates into arbitrary regular spaces. Space length ranged between 0.1m/min and 2m/min in order to avoid empty categories that cause difficulties in the subsequent analysis of log-transformed data (see Sibly et al. 1990 for a detailed description). In a next step the log transformed frequencies of steps within each movement rate category were plotted against the movement rate categories (Sibly et. al 1990). A break point in the resulting curve shows the cutoff that separates the two processes that generate movement rates. We determined the exact location of this break point using a simple maximization routine. Finally, we used equation 5 in Sibly et al. (1990) to calculate the optimal speed threshold for separating the two processes while minimizing the number of falsely assigned steps.

Defining lynx predation risk: Lynx habitat selection during long distance movements

We used a previously developed lynx resource selection function model at the home range scale to characterize spatially explicit lynx predation risk (a landscape of fear for the roe deer). We modeled time dependent lynx habitat selection during long-distance movements following the same approach as for the deer. The habitat variables considered were the same as for the deer step selection function (see table 1 in the main text). We estimated lynx home ranges from the 13 lynx by drawing a buffer of twice the mean step length around the path of each individual lynx (all data pooled) and considered the resulting polygon as the home range of each lynx (Northrup et al. 2013, DeCesare et al. 2012). From this home range we drew 10 random locations per used lynx location and separated the data set into long distance and short-distance movements based on the broken-stick model. Finally we built the resource selection functions using ordinary logistic regression. The RSF was of the form

$$w(x)= \exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n)$$

where w(x) represents the RSF score, β_0 is the intercept and the β's are the regression coefficients for the corresponding covariates ($x_1, \ldots, x_n$). Each random location was assigned a random time of day and day of year drawn from the observed lynx locations to account for the heterogenous sampling scheme of GPS fixes.

Calculating robust variance-covariance matrices for SSF model parameters sensu Forester et al. 2009

To account for serial autocorrelation in the data we calculated robust standard errors as described in Forester et al. (2009, Appendix C). We first determined the lag at which serial autocorrelation of our SSF models declined below 0.05 and subsequently clustered the data according to the determined lag. Clusters between animals were assumed independent. We then created two data sets based on every other cluster and refit the original model to each of the two datasets using the cluster() function in the survival package in R. Finally we averaged the covariance matrices of the two models and used this robust covariance matrix to calculate confidence intervals for the regression coefficients calculated for the original model.

Calculation of relative importance for the SSF models sensu Ewald et al. 2014

We tested the importance of the different model predictors as described in Ewald et al. (2014) by first randomizing each predictor variable in turn and then building models including the permutated predictor. In the end the Pearson correlations between the predictions of the true model and the model with the permutated variable was calculated. Lower correlation values

indicate greater importance. We inferred relative importance by subtracting each correlation coefficient from 1 and then scaled the results by dividing each by the sum of all those differences (table S1). We repeated this procedure 100 times and reported the average relative importance over those trials. For assessing the overall importance for the main predictor variables we performed the rescaling after summing over all predictors including the particular variable of interest (spatial and temporal interactions included; table 2 in the main text). However, we want to caution here, that this approach does not take collinearities between predictors into account and hence is not an exact measure for relative importance in the model.

Crossvalidation approach sensu Fortin et al. 2009

We performed k-fold cross-validation for a case-control design as described in Fortin et al. (2009) to assess the goodness of fit of our models. We repeatedly set aside 5 deer as the test data set and used the remaining data as the training data set. For the validation we ranked the w(x) score of the used location with respect to the random locations within each stratum (from 1-11) and subsequently recorded the frequency of occurrence of each rank within used locations. We then performed a Spearman rank correlation between the 11 ranks and the frequency of occurrence of each rank. We repeated this step 100 times, each time using a different training and test data set from all possible permutations (choosing 5 deer out of all deer with replacements) and reported the mean and range of r_s. Following Fortin et al. (2009) we did the same for a null model where we assumed a completely random pattern of habitat selection. Instead of ranking the used locations against the random locations, we ranked a randomly selected random location within each stratum against the remaining random location in the stratum (1 out of 10, excluding the used location). The rest of the procedure was identical to the one described for the used locations.

Estimating the increase in lynx predation attributable to hunting

We roughly estimated the additional lynx predation that could be attributed to hunting in order to quantify the extent of superadditive mortality. First we calculated lynx predation under hunting by summing the moving averages over the 76 day hunting period (113.7 killed deer). Then we calculated the estimated lynx predation in the absence of hunting by connecting the moving averages of predation risk between the start and end date of the hunting season with a straight line and then summed the resulting values over the 76 day hunting period (94.4 killed deer). We thereby assumed that lynx predation would follow a linear trend in the absence of hunting. In the end we calculated the estimated percental increase in lynx predation attributable to hunting by taking the ratio between the two values (113.7/94.4=1.21). Note that the absolute

number of deer killed is difficult to interpret without knowing the detection probability of deer killed by lynx.

Table S1 Model output for the hunting and non-hunting step selection function models. Corrected robust standard errors (se) are shown.

	Hunting model		Non hunting model	
Variables	coef	se	coef	se
Habitat type	0.03	0.01	0.09	0.02
House density	-0.07	0.01	-0.08	0.01
Road distance	0.21	0.01	0.21	0.02
Edge distance	-0.26	0.01	-0.26	0.01
Southern exposition	0.17	0.01	0.19	0.02
Slope	0.11	0.01	0.13	0.01
Slope sq	-0.18	0.00	-0.18	0.01
Altitude	-0.42	0.02	-0.40	0.03
Altitude sq	-0.09	0.01	-0.11	0.01
Step length	0.08	0.01	0.08	0.01
Pred. risk	-0.18	0.02	-0.25	0.03
S.expo:ytsin	0.22	0.02	0.19	0.03
S.expo:ytcos	0.25	0.02	0.25	0.02
S.expo:ytsin2	0.11	0.02	0.12	0.02
S.expo:ytcos2	-0.10	0.02	-0.14	0.03
Slope:tsin	0.10	0.01	0.10	0.01
Slope:tcos	-0.13	0.01	-0.13	0.01
Altitude:ytsin	-0.19	0.03	-0.24	0.05
Altitude:ytcos	-0.05	0.03	-0.03	0.03
Altitude:ytsin2	-0.17	0.03	-0.18	0.03
Altitude:ytcos2	-0.01	0.03	-0.03	0.04
HT:ytsin	0.13	0.02	0.01	0.03
HT:ytcos	0.04	0.02	0.05	0.02
HT:ytsin2	-0.04	0.02	-0.09	0.02
HT:ytcos2	-0.18	0.02	-0.28	0.03
HT:tsin	-0.38	0.02	-0.36	0.02
HT:tcos	0.58	0.02	0.56	0.02
House:tsin	-0.23	0.01	-0.22	0.01
House:tcos	0.17	0.01	0.17	0.01
Road:tsin	0.09	0.02	0.10	0.02
Road:tcos	-0.03	0.02	-0.05	0.02
Edge:tsin	-0.22	0.01	-0.22	0.01
Edge:tcos	0.37	0.01	0.37	0.01
Pred.risk:ytsin	0.03	0.02	0.14	0.03
Pred.risk:ytcos	-0.12	0.02	-0.16	0.02
Pred.risk:ytsin2	0.11	0.02	0.13	0.02
Pred.risk:ytcos2	-0.07	0.01	0.00	0.02
Pred.risk:tsin	-0.05	0.01	-0.05	0.01
Pred.risk:tcos	0.03	0.01	0.05	0.01

Table S2 Pearson correlations and relative importance values for each covariate of the hunting and non-hunting step selection function models.

	Hunting model		Non-hunting model	
Variables	$r_{pearson}$	rel. imp.	$r_{pearson}$	rel. imp.
Habitat type	0.9996	0.0002	0.9958	0.0019
House density	0.9893	0.0054	0.9871	0.0060
Road distance	0.8401	0.0798	0.8487	0.0705
Edge distance	0.8098	0.0950	0.8076	0.0897
Southern exposition	0.9819	0.0090	0.9781	0.0102
Slope	0.9774	0.0113	0.9709	0.0135
Slope sq	0.9233	0.0383	0.9229	0.0359
Altitude	0.6935	0.1530	0.7399	0.1212
Altitude sq	0.9781	0.0109	0.9757	0.0113
Step length	0.9720	0.0140	0.9727	0.0127
Pred. risk	0.8885	0.0557	0.7939	0.0961
S.expo:ytsin	0.9821	0.0089	1.0000	0.0000
S.expo:ytcos	0.9987	0.0007	0.9982	0.0008
S.expo:ytsin2	0.9982	0.0009	0.9918	0.0038
S.expo:ytcos2	0.9675	0.0162	0.9258	0.0346
Slope:tsin	0.8729	0.0634	0.8857	0.0533
Slope:tcos	0.7508	0.1244	0.7593	0.1122
Altitude:ytsin	0.9440	0.0279	0.9515	0.0226
Altitude:ytcos	0.9737	0.0132	0.9724	0.0129
Altitude:ytsin2	0.9876	0.0062	0.9869	0.0061
Altitude:ytcos2	0.9987	0.0007	0.9968	0.0015
HT:ytsin	0.9472	0.0264	0.9513	0.0227
HT:ytcos	0.7386	0.1301	0.7453	0.1183
HT:ytsin2	0.9732	0.0134	0.9825	0.0082
HT:ytcos2	0.9789	0.0105	0.9774	0.0105
HT:tsin	0.9944	0.0028	0.9931	0.0032
HT:tcos	0.9949	0.0026	0.9901	0.0046
House:tsin	0.9908	0.0046	0.9910	0.0042
House:tcos	0.9840	0.0080	0.9855	0.0068
Road:tsin	0.9568	0.0216	0.9488	0.0239
Road:tcos	0.9973	0.0013	0.9987	0.0006
Edge:tsin	0.9678	0.0161	0.9646	0.0165
Edge:tcos	0.9999	0.0000	0.9989	0.0005
Pred.risk:ytsin	0.9984	0.0008	0.9481	0.0242
Pred.risk:ytcos	0.9833	0.0083	0.9626	0.0174
Pred.risk:ytsin2	0.9776	0.0112	0.9649	0.0164
Pred.risk:ytcos2	0.9919	0.0040	1.0000	0.0000
Pred.risk:tsin	0.9958	0.0021	0.9954	0.0022
Pred.risk:tcos	0.9979	0.0011	0.9937	0.0029

Table S3 Model output for the hunting and non-hunting LOGIT models for roe deer. Corrected robust standard errors (se) are shown.

	Roe deer models			
	Hunting model		Non-hunting model	
Variables	coef	se	coef	se
Intercept	-0.179	0.012	-0.225	0.015
Habitat type	0.721	0.015	0.821	0.020
Pred.risk	-0.053	0.012	-0.015	0.017
House density	0.004	0.007	0.001	0.008
Road density	-0.004	0.006	-0.013	0.007
Altitude	0.016	0.007	-0.009	0.010
Altitude sq	-0.006	0.004	-0.001	0.005
Slope	0.004	0.006	0.004	0.007
Slope sq	-0.038	0.004	-0.039	0.004
Edge distance	0.019	0.006	0.023	0.006
Southern exposition	0.089	0.012	0.112	0.017
tsin	-0.142	0.009	-0.131	0.010
tcos	0.197	0.015	0.126	0.016
ytsin	-0.043	0.010	-0.041	0.018
ytcos	-0.185	0.011	-0.210	0.012
ytsin2	-0.060	0.011	-0.055	0.013
ytcos2	0.185	0.010	0.181	0.015
HT:tsin	-0.011	0.014	-0.023	0.015
HT:tcos	-0.007	0.023	0.001	0.024
HT:ytsin	0.092	0.016	-0.036	0.027
HT:ytcos	0.303	0.017	0.341	0.019
HT:ytsin2	0.052	0.015	0.001	0.018
HT:ytcos2	-0.245	0.015	-0.316	0.021
House:tsin	-0.027	0.007	-0.024	0.008
House:tcos	-0.072	0.010	-0.075	0.011
Road:tsin	0.018	0.006	0.020	0.007
Road:tcos	-0.018	0.009	-0.010	0.010
Altitude:ytsin	0.063	0.009	0.093	0.015
Altitude:ytcos	0.018	0.008	0.013	0.009
Altitude:ytsin2	0.005	0.009	0.020	0.010
Altitude:ytcos2	0.041	0.008	0.053	0.012
Slope:tsin	-0.028	0.007	-0.024	0.007
Slope:tcos	0.102	0.010	0.104	0.010
Edge:tsin	0.026	0.006	0.025	0.007
Edge:tcos	-0.124	0.009	-0.124	0.010
S.expo:ytsin	0.061	0.017	0.004	0.028
S.expo:ytcos	0.097	0.016	0.100	0.016

S.expo:ytsin2	0.044	0.016	0.038	0.019
S.expo:ytcos2	0.031	0.015	-0.003	0.022
Pred.risk:tsin	-0.011	0.007	-0.020	0.008
Pred.risk:tcos	-0.280	0.012	-0.263	0.013
Pred.risk:ytsin	-0.079	0.011	-0.101	0.020
Pred.risk:ytcos	-0.038	0.012	-0.017	0.014
Pred.risk:ytsin2	-0.009	0.010	-0.020	0.012
Pred.risk:ytcos2	-0.057	0.010	-0.056	0.014

Table S4 Model output for the hunting and non-hunting LOGIT models for lynx. Corrected robust standard errors (se) are shown.

	Lynx models			
	Hunting model		Non-hunting model	
Variables	coef	se	coef	se
Intercept	0.066	0.066	-0.110	0.088
Habitat type	0.600	0.077	0.728	0.102
Pred.risk	-	-	-	-
House density	0.079	0.034	0.080	0.036
Road density	-0.078	0.039	-0.083	0.041
Altitude	0.092	0.049	-0.004	0.064
Altitude sq	0.059	0.027	0.068	0.029
Slope	-0.118	0.027	-0.101	0.028
Slope sq	-0.016	0.014	-0.020	0.015
Edge distance	0.136	0.108	0.077	0.112
Southern exposition	-0.126	0.072	0.047	0.103
HT:Edge distance	-0.169	0.117	-0.104	0.122
House density:Road dist.	-0.021	0.033	-0.002	0.035
tsin	0.034	0.034	0.051	0.036
tcos	0.302	0.060	0.308	0.063
ytsin	-0.187	0.064	0.126	0.117
ytcos	0.083	0.080	0.013	0.090
ytsin2	-0.202	0.064	-0.084	0.080
ytcos2	-0.020	0.062	0.165	0.082
HT:tsin	-0.156	0.054	-0.187	0.057
HT:tcos	0.338	0.086	0.295	0.089
HT:ytsin	-0.096	0.080	-0.282	0.137
HT:ytcos	0.117	0.101	0.176	0.112
HT:ytsin2	0.139	0.080	0.057	0.096
HT:ytcos2	-0.086	0.083	-0.175	0.107
House:tsin	-0.121	0.029	-0.129	0.031
House:tcos	0.104	0.042	0.119	0.043
Road:tsin	-0.003	0.029	-0.014	0.031

Road:tcos	-0.018	0.042	-0.021	0.044
Altitude:ytsin	-0.065	0.054	0.104	0.081
Altitude:ytcos	-0.035	0.060	-0.076	0.066
Altitude:ytsin2	-0.098	0.050	-0.024	0.060
Altitude:ytcos2	0.031	0.049	0.124	0.059
Slope:tsin	0.108	0.027	0.120	0.029
Slope:tcos	-0.043	0.036	-0.032	0.037
S.expo:ytsin	0.125	0.094	-0.175	0.154
S.expo:ytcos	-0.120	0.100	-0.015	0.114
S.expo:ytsin2	0.083	0.088	-0.062	0.104
S.expo:ytcos2	-0.001	0.087	-0.157	0.111

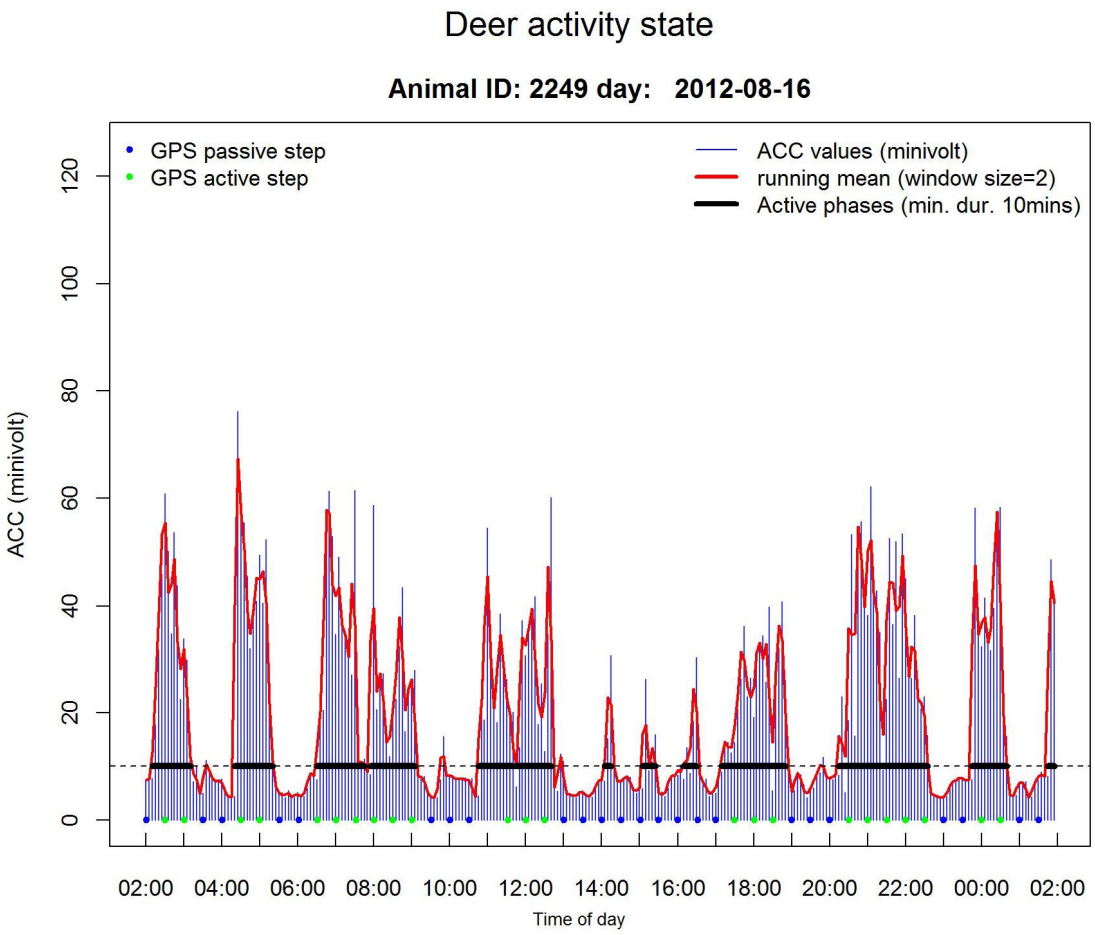

Figure S1 Plot of the acceleration data used to separate deer steps into active and passive state (ACC; in millivolts) for individual 2249 on August 16 2012. Blue bars denote the acceleration raw data (in millivolt) whereas red shows the moving average for a window size of 2 (2x5 minutes). The black dotted line indicates the 10 millivolt threshold that was used for assigning activity state. The horizontal black bars denote the active periods with a minimum length of 10 minutes. Blue and green dots show the GPS locations for passive and active periods respectively.

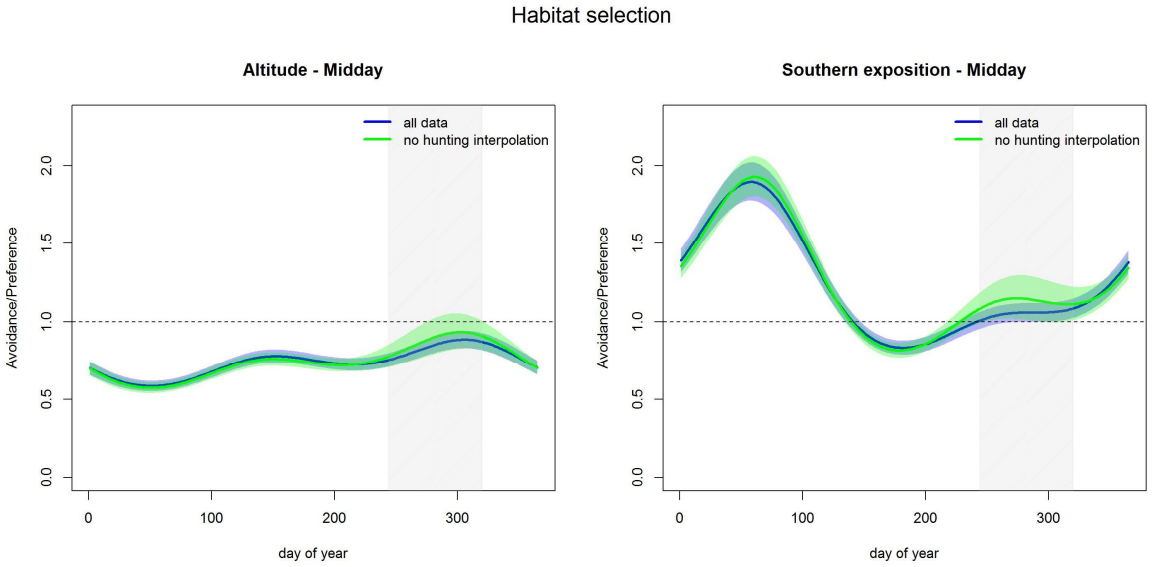

Figure S2 Selection of altitude (left panel) and southern exposed slopes (right panel) shown for midday. Blue curves show the w(x)=exp(coef) values of the SSF for the hunting model whereas green curves indicate w(x) for the non-hunting model. The colored shaded areas denote the robust 95% -pointwise confidence intervals for the hunting model (blue) and the non-hunting model (green). For the calculation of the effect displays all predictors were set to 0 (continuous predictors were standardized) except for altitude (left panel) and southern exposed slopes (right panel). The shaded area in grey depict the 10 week hunting period in fall. The dotted line for w(x)=1 represents no selection/avoidance. The response to altitude denotes the selection/avoidance of high altitudes (75% quantile) relative to the mean altitude over the course of the year. The response to southern exposed slopes denotes the selection/avoidance of southern exposed slopes relative to other expositions over the course of the year.

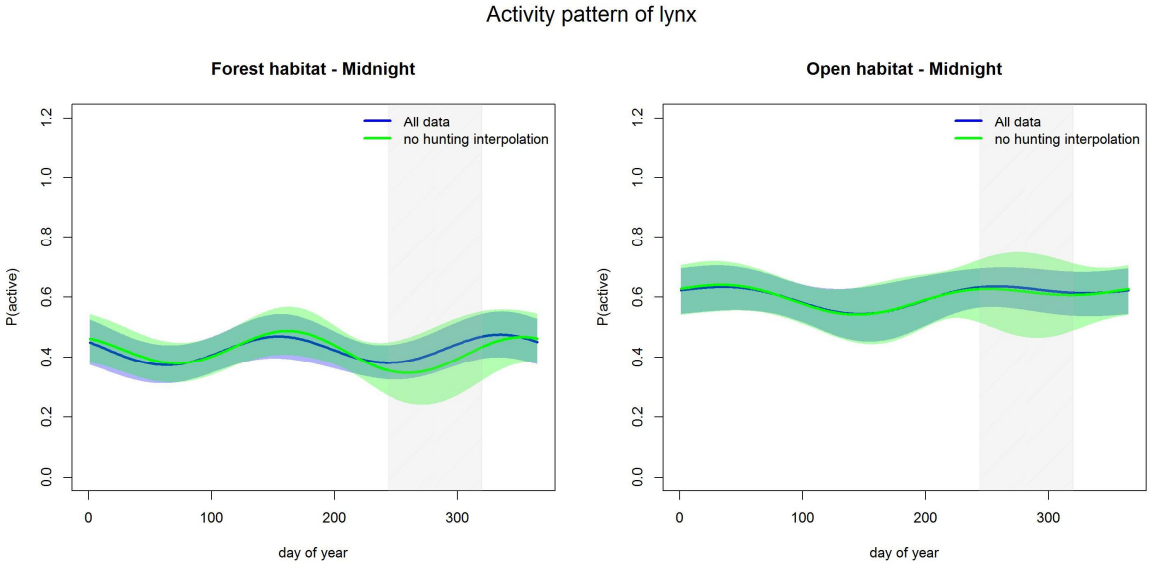

Figure S3 Activity patterns of lynx in the forest (left panel) and in open habitat (right panel) during nighttime over the course of the year. The results show the probability of a lynx being active while setting all other covariates to 0 (continuous predictors were standardized). Blue curves show the activity for the full data model, green curves for the non-hunting model. The colored shaded areas denote the robust 95% -pointwise confidence intervals for the hunting (blue) and the non-hunting model (green). The shaded area in grey depicts the 10 week hunting period in the fall.

References

DeCesare, N. J., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. - Ecological Applications 22: 1068-1083

Forester, J.D., Im, H.K. & Rathouz, P.J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*, 90, 3554-3565.

Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology*, 90, 2480-2490.

Ewald, M., Dupke, C., Heurich, M., Mueller, J. & Reineking, B. (2014). LiDAR Remote Sensing of Forest Structure and GPS Telemetry Data Provide Insights on Winter Habitat Selection of European Roe Deer. *Forests*, 5, 1374-1390.

Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. - Ecology 61: 65-71.

Northrup, J. M., et al. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. - Ecology 94: 1456-1463.

Sibly, R. M., et al. 1990. Splitting behavior into bouts. - Animal Behaviour 39: 63-69.

Chapter 3
Strong non-consumptive effects of a large mammalian ambush predator reduce the survival of one of its main prey

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Abstract

The impact of predators on their prey goes beyond their consumptive effects. By changing the behavior and space use patterns of their prey, predators evoke non-consumptive effects (NCE) in their prey that may affect the preys survival and reproduction. The strength of such NCE depends largely on the hunting mode of the predator. Ambush predators exert stronger NCE than active predators as they provide more persistent cues about predation risk than their widely roaming counterparts. While evidence comes from different taxonomic groups, evidence from large mammalian predator-prey systems is rare and equivocal. In this study we looked at the occurrence and strength of NCE of the ambush predator, the Eurasian lynx (*Lynx lynx*) on one of its main prey the European roe deer (*Capreolus capreolus*) and tested for knock on effects on deer survival. Prey respond to spatial and temporal variation in risk according to the risky places and risky times hypothesis. Thus we tested how roe deer respond to long term levels of chronic lynx predation risk (risky places) and how their antipredator behavior changes under acute predation risk when a lynx is in close proximity (risky times). Finally we tested whether these NCE affected non-lynx predation related mortality. We found strong NCE in roe deer in response to both risky places and risky times. Furthermore this response was dependent on season and time of day. Finally the observed NCE were strong enough to exert knock on effects on deer survival. In accordance with ecological theory we found strong NCE of a large mammalian ambush predator on one of its main prey. Together with others, these findings suggest that the occurrence of strong NCE should also be common in large mammalian predator-prey systems. Furthermore we show that NCE may strongly depend on the spatiotemporal distribution of risks as well as the environmental context. There is a need for studies looking at NCE over multiple prey populations exposed to different levels of predation and in different environmental contexts to shed more light on the processes determining the strength of NCE in large predator-prey system with different predator types.

Keywords: Cox proportional hazards model, hunting mode, lynx, predation risk, roe deer, step selection function

Introduction

Understanding predator-prey interactions is a central concern in Ecology. There is a large body of literature showing that the impact of predators on their prey goes beyond their consumptive effects (CE; Lima&Dill 1990, Dill Lima 1998). The ecology of fear predicts that fearful prey respond to the presence of predators thereby reducing their exposure to predation risk (Brown et al. 1999). Behavioral responses to predator presence often comes at the cost of reduced feeding rates, changes in diet or increased stress levels which can alter prey survival and reproduction (Lima&Dill 1990). An increasing body of literature shows that such non-consumptive effects (NCE) of predators are important in shaping population dynamics of prey species and may even outweigh the consumptive effects in the long run (reviewed in Brown&Kotler 2004, Preisser et al. 2005, Peckarsky et al. 2008).

The relative importance of non-consumptive effects is determined by different factors of which the hunting mode of the predator was found to be the most important, irrespective of taxonomic group (Preisser et al. 2007, Schmitz 2008). Ambush predators are predicted to have stronger NCE because their stable territory and space use provides more reliable and persistent cues about predation risk that can be associated with specific habitat features by the prey. Widely roaming and actively hunting predators in contrast should provide more variable and less predictable information about local predation risk and therefore evoke less response in their prey (Schmitz et al. 2005, Preisser et al. 2007, but see Weissburg et al. 2014). Only few studies have tested this prediction for large mammalian predator-prey systems and results have been equivocal. A behavioral study in a multiple predator prey system in South Africa found that ungulates showed a stronger avoidance response to ambush predators such as lions than to active predators such as wild dogs (Thaker et al. 2011). Another study on an African ungulate community and its predators, however found stronger NCE from the actively hunting spotted hyenas than from lions (Creel et al. 2014). In addition several single-predator studies have found strong NCE for both ambush predators such as lions or Canadian lynx (Peckarsky et al. 2008, Valeix et al. 2009, Periquet et al. 2012), as well as for actively hunting wolves in North America (e.g. Creel et al. 2005, Fortin et al. 2005, Christianson&Creel 2010). Thus, evidence from large mammalian predator-prey systems that ambush predators have stronger NCE is equivocal and there have been doubts about the general applicability of this prediction to these systems (Creel et al. 2013, Creel et al. 2014, Weissburg et al. 2014).

The ecology of fear assumes that prey individuals have some information about their current risk level (Brown et al. 1999). Predation risk varies both in space and time. Temporal variation in risk is dependent on predator space use (presence or absence) as well as on external factors such as light conditions or snow cover which may change the success rate of a predator (Lima&Dill 1990). On the other hand spatial variation in risk is more a function of predator habitat selection and specific habitat features associated with varying attack success. In this context the *risky times*

hypothesis is concerned with the response of prey to temporal variation in predation risk as a function of predator presence or absence whereas the *risky places hypothesis* predicts that prey assess predation risk by the long term level of risk associated with particular habitat features (Creel et al. 2008). In either case prey may prevent being killed by increasing vigilance (Laundre et al. 2001) or reducing activity (Kotler et al. 1992), by avoiding the preferred habitat of predators (predator habitat selection; Hebblewhite et al. 2005, Atwood et al. 2009) or by avoiding habitats that increase the risk of being killed when encountering a predator (risky habitat; Thaker et al. 2011).

The risky places and risky times hypotheses are not mutually exclusive and studies have found evidence for both (e.g. Fortin et al. 2005, Creel et al. 2014). Nonetheless, the two hypotheses are only rarely considered concurrently (but see Valeix et al. 2009, Creel et al. 2014). In this study we tested how roe deer respond to long term levels of chronic lynx predation risk (risky places) and how their antipredator behavior changes under acute predation risk when a lynx is in close proximity (risky times). In general we expected the response to risky times to occur at small scale by changes in habitat selection rather than movements away from nearby predators because roe deer territories are small and the possibility to move away from a predator is therefore limited. For this reason we simply tested whether deer responded differently to chronic predation risk depending on the acute presence or absence of a lynx. Furthermore we looked at whether deer shifted their habitat use to safer places or reduced their activity under acute predation risk when a lynx is present.

At last, we asked if NCE were strong enough to affect roe deer survival by analyzing whether deer living in areas with more risky places suffered from higher non-lynx predation related mortality than deer from areas with less risky places. To get an idea about the relative importance of these effects we contrasted NCE from lynx to direct and indirect effects of humans on these mortalities.

In summary we tested the following four predictions: 1) Roe deer avoid areas of high chronic predation risk from lynx according to the risky places hypothesis. 2) Roe deer avoid high chronic predation risk more during acute predation risk when a lynx is currently present according to the risky times hypothesis. 3) Roe deer will shift their habitat use to safer places and reduce their activity during acute predation risk according to the risky times hypothesis. 4) Roe deer living in high predation risk areas suffer from increased non-lynx related mortality due to NCE.

In this study we show that the behavioral response leading to NCE effects in the lynx-roe deer predator-prey system are strong enough to affect deer survival. These findings are in line with ecological theory predicting strong NCE for ambush predators such as the Eurasian lynx. We discuss the potential impact of reduced survival on roe deer demography and suggest future studies to unravel the mechanisms that determine the strength of NCE in large mammalian ambush predators.

Methods

Study area

This study was conducted in the Northwestern Swiss Alps (NWSA). The study area covered roughly 1500km^2 (center coordinates 46.559905 N, 7.513052 E) and ranged in altitude between 600m and 3500m a.s.l. Most human settlements (33 inhabitants/km^2) in the region are situated at the valley bottoms. Valley bottoms and lower slopes have been deforested since the middle ages for agricultural use. Remaining forests (about 30% of the total area) are situated mostly on the higher slopes and are highly fragmented. The treeline lies between 1800m and 1950m. The entire region is used intensively for recreational purposes (Pesenti and Zimmermann 2013). Besides outdoor tourism such as hiking and skiing, hunting is an important activity among local people. The hunting season on chamois *(Rupicapra rupicapra*) and red deer (*Cervus elaphus*) lasts all of September, whereas roe deer hunting is restricted between October 1 and November 15. Lynx density in the region was estimated at 2.05 independent lynx/100 km^2 from a camera-trapping census in winter 2013/14 (Zimmermann et al. 2014). Roe deer (36% of identified kills) and chamois (39%; KORA, unpublished data) are the main prey items of the lynx in the study area.

Animal captures and data collection

Between November 2011 and April 2013 we captured roe deer (n=65) using drive nets or box traps and equipped them with GPS collars (e-obs GmbH, Gruenwald, Germany) recording locations every 30 minutes (n=1'351'368 locations). Because mean GPS error (27m) was large with respect to the mean step length of 54m (Visscher 2006) we rarefied the data to 2h fix intervals resulting in a data set with 302'633 deer locations (mean step length=123m). Simultaneously, 13 lynx were GPS-collared in our study area, yielding 18'910 GPS locations of lynx during the same period. Capture protocol and data collection for lynx are described elsewhere (Gehr et al. in review).

Measuring chronic and acute predation risk

Chronic predation risk

To characterize the response of roe deer to the chronic background level of predation risk by lynx (according to the risky places hypothesis) we used a previously developed habitat selection model for lynx in the study area (Gehr et al. in review). For this model we built a resource selection function to model temporal dynamics in habitat selection of lynx and then used these lynx resource selection function values at each deer location (w(x)) to define the landscape of lynx predation risk for the deer. Zimmermann et al. (2014) found that lynx occurred across our entire study area. Hence, the lynx resource selection function values at each deer location would

seem to be a reasonable estimate of the long-term, average lynx predation risk. In the following we refer to this as the chronic predation risk.

Acute predation risk

To assess the response of roe deer to the immediate passage of a lynx (acute predation risk during risky times) we searched the combined lynx and roe deer location data set for close encounters between collared lynx and collared deer. For this purpose, we first defined an encounter in terms of distance and time between predator and prey. Different studies have looked at the response of ungulate prey to the immediate presence of large predators such as wolves or lions (e.g. Valeix et al. 2009, Periquet et al. 2012, Latombe et al. 2014, Basille et al. 2015). Even though the response to the recent passage of a predator has been found to carry for several kilometers and lasted for several days, we expected the strongest response within the first 1-2km and 24-48 hours (Middleton et al. 2013). We therefore defined an encounter as a situation when a lynx was present within 1km of a deer within 24 hours and referred to this as acute predation risk.

Modelling the response of deer to risky places and risky times using step selection functions

We used step selection functions to test how roe deer respond to risky places and risky times and looked at how chronic and acute predation risk interact in shaping roe deer antipredator behavior. We first outline the statistical approach and then introduce important habitat variables in general involved in roe deer habitat selection. In the end we explain how we tested the response of roe deer to chronic and acute lynx predation risk with respect to predictions 1-3 outlined in the introduction.

Separating animal paths into steps

For the analysis of habitat selection animal paths were broken down into successive steps. Each step was characterized by the step length (the straight-line segment between two successive locations) and the turning angle (the angle between the previous and the current step). Each step was then assigned habitat variables and predation risk found at the end of the step. Encounters between lynx and roe deer were defined at the beginning of a step in order to measure the response of the deer to the encounter at the end of the step (see next section for details). . Following this approach we calculated for each roe deer step the time and distance to all lynx locations that fell within the constraints outlined above. If more than one lynx location complied with the distance/time constraints only the most recent location was kept. To find encounters we restricted our analysis to lynx and deer whose 100% minimum convex polygons (MCP) overlapped (n_{Lynx}=13, n_{Deer}=58).

Independence of movements between collared roe deer

During the study several collared deer formed transient coalitions for extended time periods. Hence, we could not assume independence of movements between all animals at all times which is relevant for habitat selection analysis outlined in the following section. To identify deer pairs we calculated the distance between concurrent locations of all deer with overlapping 100% MCP (Fortin et al. 2005). We considered deer movements to be independent, when animals were further apart than 50m from each other and dependent otherwise. Roughly 12% of all steps were paired steps. We accounted for non-independence between paired steps by calculating robust variance estimators in step selection function (see below).

Step selection function modelling

We analyzed the response of roe deer to chronic and acute lynx predation risk using step selection functions (SSF; Fortin et al. 2005). Each realized step of the final datasets was paired with 10 alternative random steps which shared the same origin but had different end points. Random step lengths and turning angles were drawn in pairs from the empirical distributions in the data (Thurfjell 2014). These case-control data consisting of realized and random steps were then analyzed using conditional logistic regression.

Successive steps in SSF cannot be considered independent (reviewed in Fieberg et al. 2010). We used the autocorrelation in the deviance residuals to determine the lag after which steps could be considered independent (Fortin et al. 2005). Analysis of the movement statistics in the raw data indicated strong circadian patterns in the step lengths that persisted in the deviance residuals of the SSF models. Including an interaction of step length with a cosine function of time of day (cosine(time/(24/constant), where the constant adjusts for the period of the cycle in the dataset) reduced but did not completely remove the circadian patterns in the deviance residuals of the SSF. Hence we also divided the data into day and night based on sun angle (sun angle >0=day and night otherwise) and analyzed the two datasets separately (van Beest et al. 2012). We considered autocorrelation in the deviance residuals to be negligible when values dropped below 0.1. After splitting the analyses into day and night, no autocorrelation remained in the deviance residuals of the night data set (Figure S1a supporting information). In the day model, autocorrelation became negligible beyond lag 24 (48 hours; Figure S1b supporting information). We estimated robust variances for day-regression coefficients by creating independent clusters of correlated steps following the procedure described in Forester et al. (2009). We accounted for non-independence of paired steps between deer by randomly selecting one step per pair and removing the other. We then calculated robust variances from this reduced dataset.

To test the fit of the models we performed cross validations for case-control designs for the day and night model as described in Fortin et al. (2009). Instead of dividing the data randomly we removed groups of 5 individuals as the test dataset and built the SSF on the remaining deer (see

Gehr et al. in review for details). We report the average spearman rank correlation (r_s) over 100 trials with associated 95% confidence intervals. High r_s is indicative of a good model fit.

All continuous covariates were standardized (mean of 0 and SD of 1) except for the cosine function for time of day. We used variance inflation factors (VIF) to test for multicollinearities between all model covariates. VIF-values larger than 2 could all be attributed to the inclusion of interactions and power transformations (max VIF was 4.6 for the altitude-season interaction). Therefore we considered multicollinearity to be a minor issue in our models (Zuur et al. 2009).

Habitat variables

We included habitat variables in the SSF that are known to be important for roe deer. Roe deer occur at high densities in fragmented cultivated land where they are closely associated with forest edges at the interface of open habitat and forest (Danilkin 1996). Open habitats provide rich feeding opportunities for deer but are associated with high human disturbance (Hewison et al. 2001). Therefore open habitat was included as a dummy variable with 1=open and 0=forest. We further included distance to the closest forest edge to account for the fact that deer may evaluate risk in the open depending on the distance to cover. We included house density as well as proximity to roads asboth variables strongly affect roe deer habitat selection (e.g. Coulon et al. 2008). Furthermore we included altitude and slope, since altitude correlates with climate variables and steep slopes have been associated with low human activity in previous studies and may serve as a refuge for roe deer (Zimmermann et al. 2002, but also see Lone et al. 2014). For both altitude and slope a quadratic term was included to allow for non-linear effects of these habitat variables. Finally southern exposed slopes (dummy variable with 1=southern exposed slope and 0=all other directions) may be preferred by ungulates during winter because this is where snow cover first disappears (e.g. Plank 2013).

Temporal variables

Habitat selection of roe deer differs between day and night, according to differences in human activity and predation risk (Hewison et al. 2001, Padie et al. 2015). By running separate SSF models for day and night we accounted for daytime differences in habitat selection. Moreover, as snow cover is known to affect habitat selection as well as predation risk (Mysterud et al. 1999) we differentiated two seasons according to months during which snow typically may occur and months which are mostly snow free. Accordingly we defined beginning of November until end of April as the winter season and beginning of May until end of October as the summer season. Because season is constant across a stratum of 1 used and 10 associated random steps, and because conditional logistic regression does not allow to fit main effects for predictors that are

constant within stratum, we included season only as an interaction with the habitat variables in the SSF model.

We did not expect selection of all habitat covariates to depend on season. We expected selection of slope, distance to forest, house density and road distance to mainly depend on human disturbance which itself mostly follows circadian rather than seasonal fluctuations. Hence we did not fit interaction terms with season for those 4 habitat variables.

Response to risky places and risky times: interaction of chronic and acute predation risk

In the end we used the chronic and acute lynx predation risk to model the response of roe deer to risky places and risky times. We tested for the response of deer to risky places with the main effect of chronic lynx predation risk (*prediction 1*). In addition we included an interaction term between chronic predation risk and acute predation risk to test whether deer avoided chronic risk areas more during risky times when a lynx was present (*prediction 2*). Because associated realized and random steps shared the same acute predation risk (0=no encounter in the past 24h within 1km, 1=encounter in the past 24h within 1km) no main effect for encounter was used in the models. Moreover a main effect for encounter would have tested whether deer are less likely to use a location when a predator is nearby which we didn't expect given the small territory size of roe deer and their accordingly limited possibility to move away. For *predication 3* we tested whether roe deer were selecting for safer habitat or reducing their activity during acute predation risk (risky times). In our study site 70% of 201 kills from collared lynx were found in the forest (KORA, unpublished data) whereas only 44% of all lynx locations and 41% of all deer locations were inside the forest. Furthermore kills were found in steeper terrain and closer to forest edges than expected from random locations. Thus we included interaction terms for acute predation risk with open habitat, distance to forest edge and slope in our SSF models. Furthermore we included an interaction term between encounter and step length to test whether deer changed their activity during acute predation risk (e.g. Basille et al. 2015). Finally we included an interaction between season and chronic predation risk as we were interested if avoidance to risky places differs between winter and summer.

Impact of non-consumptive effects on deer survival using cox models

At last we wanted to test whether NCE affect deer survival in accordance with prediction 4 in the introduction. To answer this question we built cox regression models using mortality data from collared roe deer. In the following we first describe the mortality data and then specify the cox proportional hazard models.

Mortality data

All collars were equipped with a mortality switch (mortality delay between 4-6 hours) that allowed to assess time and cause of death. Deer survival was checked every other day. For natural mortalities other than lynx predation the carcasses were brought to the Centre for Fish and Wildlife Health at the University of Bern, Switzerland to determine cause of death. In the case of lynx predation the carcasses were not removed from the site to avoid increasing the hunting efforts of lynx, which could result from kill removal. Hunted animals were reported by the hunters. Mortalities (n=40) were separated into hunting (n=12 or 30% of all mortalities, including two poached deer), lynx predation (n=10, 25%), dog predation (n=2, 5%), disease and starvation (n=7, 17.5%), road kills (n=2, 5%) and unknowns (n=7, 17.5%). Unknown mortalities were unlikely due to lynx predation, as lynx killed deer are usually consumed over several days, or due to poaching as poached animals are likely to be removed from the crime site (but see below).

Cox regression modeling

We tested for non-consumptive effects of lynx predation risk on deer survival using cox proportional hazard models. We were interested in testing whether deer exposed to higher chronic predation risk by lynx suffered from higher non-lynx predation related mortality as a cost from chronic stress or anti-predator behavior. Thus we calculated for each deer the mean chronic predation risk. We did this over all used and random locations in order for predation risk to represent what is available to the deer. To get an idea about the relative importance of NCE on deer survival we contrasted these NCE of lynx to the direct (road kills, dog predation and possibly unknown mortalities) and indirect (disease, starvation and unknown mortalities) effects of human disturbance since lynx and human-related mortalities are the major determinants of roe deer deaths. We excluded hunting mortalities due to difficulties in dealing with pulsed mortality causes in Cox proportional hazard models. As a proxy for human disturbance we calculated for each deer the mean distance to the closest road for all used and random steps analogous to the mean chronic predation risk (Coulon et al. 2008). For the analysis we log-transformed the distance to the road. Because altitude positively correlates with chronic predation risk (r=0.69), we also included altitude as a covariate in the models. We built 3 candidate models (table 1) considering chronic predation risk and human disturbance separately or in combination with each other and selected the most appropriate model explaining survival patterns using AIC scores (Burnham&Anderson 2002). Altitude was kept as a predictor in all three models tested due to the correlation between altitude and predation risk. To explore the functional form of the relationship between the predictor variable and the hazard function, we plotted the martingale residuals of the null model (β=0) against each of the three predictors separately and superimposed a scatterplot smooth (Therneau&Grambsch 2000; Figure S2 supporting information). We used a staggered entry design using daily encounter histories (see above). We

parametrized the mortality data from all 65 deer as follows: all mortalities excluding mortalities from lynx predation and hunting were assigned as mortalities (18 mortalities), whereas lynx kills and hunted animals were entered as censored observations. Unknown mortalities were considered as natural mortalities in these analyses because they were unlikely related to lynx predation or hunting. However, excluding unknown mortalities did not change the results of the analyses (data not shown here). The proportional hazard assumption was tested using scaled Schoenfeld residuals (cox.zph function, Fox 2002). Influential points were identified by plotting the transformed score residuals against the individual model predictors (Therneau&Grambsch 2000).

All statistical analyses were conducted using R (R Core Team 2014).

Results

We found pronounced variation in exposure to chronic predation risk among radio-collared deer. The lowest and highest mean chronic predation risk of individual deer differed by a factor 5.7 and ranged between 0.06 and 0.31. Roughly 2% of all deer steps were associated with acute predation risk during which a collared lynx was closer than 1km within the past 24 hours. During the closest encounter a lynx came within 21m of a roe deer with a time delay of 11 hours. During the closest real time encounter (time delay=0) a lynx came within 180m of a collared roe deer. The average encounter distance was 712m with an average time delay of 10hours.

Modelling the response of deer to risky places and risky times using step selection functions

Cross-validation results for the day and night SSF model, respectively, indicated good model fit and differed significantly from the null model of random space use (mean $r_{s\text{-}DAY\text{-}used}$=0.999 vs mean $r_{s\text{-}DAY\text{-}random}$=0.332; mean $r_{s\text{-}NIGHT\text{-}used}$=0.885 vs mean $r_{s\text{-}NIGHT\text{-}used}$=0.316). In general habitat selection of roe deer differed markedly between day and night as well as between the summer and winter season (table 2). During the day roe deer strongly avoided open habitat and proximity to human features, represented by house density and distance to the closest road. During the night deer spent more time in the open closer to houses and roads and also at further distances from the forest edge. Furthermore roe deer preferred less steep slopes during the night than during the day.

In summer deer spend more time in the open than during winter and this pattern is particularly strong at night. In contrast, roe deer select for southern exposed slopes during winter but not during summer. Finally roe deer seemed to select for intermediate altitudes in winter during the day whereas in summer and during the night in general deer preferred low altitudes.

Response to risky places and risky times: interaction of chronic and acute predation risk

Roe deer avoided chronic lynx predation risk in general according to the risky places hypothesis (*prediction 1*), however the response was also strongly dependent on the time of day and season. During the day, roe deer avoided chronic lynx predation risk during both winter and summer (table 2, Figure 1a). At night, on the other hand, deer strongly avoided chronic predation risk during summer but seemed to select for it in winter (Figure 1b).

Roe deer also responded to risky times under acute predation risk: in a situation of acute predation risk roe deer avoided chronic predation risk more during the night (according to *prediction 2*) whereas during the day there was no response (Figure 2). In addition to an increase in avoidance of chronic predation risk deer also shifted their habitat use and reduced their activity during acute predation risk which was in line with *prediction 3* (Figure 3). More specifically, during the day roe deer avoided open habitat further away from forest edges less when they were under acute predation risk. During acute predation risk at night deer also increased their use of open habitat but the distance to forest edges remained unchanged. Finally deer also slightly reduced their movements when a lynx was in close proximity at night which was not the case during the day (table 2).

Impact of non-consumptive effects on deer survival using cox models

We tested the impact of NCE on deer survival using a cox model for all natural mortalities excluding lynx predation. The cox model with the lowest AIC score included all three predictors: mean distance to roads, mean altitude and mean chronic predation risk (table 1). Inspection of the Schoenfeld residuals indicated no violation of the proportional hazard assumption. We identified four putatively influential points for chronic predation risk. Removing these points did not change the results of the cox model. According to *prediction 4* we found that living in areas of high chronic predation risk (risky places) was associated with increased non-lynx-related mortality risk (HR=4.75, $p<0.000$). In contrast the hazard decreased with increasing distance to roads (HR=0.32, $p=0.002$) meaning that the mortality risk was higher when mean distance to roads was low. The comparison of the NCE of lynx with the direct and indirect effects from human disturbance showed that NCE had a stronger impact than human disturbance (a unit change in mean chronic predation risk increased the hazard 4.75 times whereas a unit decrease in mean log distance to roads increased the hazard by only 3.17 times (1/0.315). Finally, living at higher altitudes reduced the hazard of dying from non-lynx predation related mortality (HR=0.53, $p=0.053$).

Table 1 Model selection of three Cox models looking at the effect of mean distance to roads and mean chronic predation risk (chronic PR) on the hazard ratio for deer mortality while accounting for mean altitude. Mean distance to road was log-transformed (Log(Road)).

Model	LL	K	AICc	ΔAICc	ω
Log(Road)+chronic PR+Altitue	-100.920	3	208.233	0.000	0.965
Log(Road)+Altitue	-105.532	2	215.258	7.025	0.029
Chronic PR+Altitue	-107.091	2	218.376	10.144	0.006

Table 2 Model output of the two step selection function models for day and night. Model coefficients together with standard errors and 95%-confidence intervals are shown. For the day model the model standard errors are reported together with the robust standard errors. For the night model the model standard errors were used to calculate confidence intervals as there was no residual autocorrelation in the deviance residuals of the model.

	SSF Day					SSF Night			
Variables	β	model_se	robust_se	Lower CI	Upper CI	β	robust_se	Lower CI	Upper CI
Habitat type	-0.665	0.013	0.037	-0.738	-0.592	-0.1699	0.01073	-0.19094	-0.14886
Road distance	0.247	0.009	0.017	0.214	0.281	0.27419	0.00952	0.25553	0.29285
House density	-0.199	0.006	0.011	-0.221	-0.177	0.01146	0.00584	1.00E-05	0.02292
Exposition	0.171	0.013	0.025	0.122	0.220	0.24792	0.01132	0.22574	0.2701
Edge distance	-0.563	0.006	0.016	-0.595	-0.530	0.01637	0.00399	0.00856	0.02419
Slope	0.159	0.005	0.010	0.140	0.178	-0.01	0.00441	-0.01864	-0.00137
Slope sq	-0.151	0.003	0.006	-0.162	-0.140	-0.12971	0.00313	-0.13584	-0.12358
Altitude	0.131	0.027	0.050	0.033	0.230	-1.21537	0.0247	-1.26378	-1.16696
Altitude sq	-0.306	0.017	0.030	-0.365	-0.248	0.00787	0.01393	-0.01944	0.03517
Step length	-0.017	0.003	0.008	-0.034	-0.001	0.00052	0.00306	-0.00549	0.00652
Predation risk	-0.080	0.009	0.020	-0.120	-0.040	0.13573	0.00748	0.12107	0.15038
Hab. type:season	0.051	0.017	0.044	-0.036	0.138	0.5679	0.01563	0.53727	0.59853
Hab. type:acute PR	0.190	0.059	0.107	-0.019	0.400	0.15854	0.05591	0.04895	0.26812
Edge dist:acute PR	0.162	0.040	0.085	-0.003	0.328	0.0377	0.02718	-0.01557	0.09097
Slope:acute PR	-0.063	0.028	0.055	-0.170	0.043	0.06894	0.028	0.01407	0.12382
Exposition:season	-0.260	0.017	0.032	-0.323	-0.198	-0.23579	0.01654	-0.26821	-0.20338
Altitude:season	-0.482	0.035	0.064	-0.607	-0.356	0.62046	0.03838	0.54524	0.69568
Altitude sq:season	0.261	0.020	0.034	0.194	0.328	-0.0567	0.01779	-0.09157	-0.02184
Step length:tcos	-0.236	0.004	0.008	-0.252	-0.220	-0.1799	0.00426	-0.18825	-0.17156
Step length:acute PR	0.023	0.019	0.038	-0.052	0.098	-0.07055	0.01954	-0.10885	-0.03225
Pred. risk:season	0.028	0.013	0.027	-0.026	0.081	-0.3601	0.01844	-0.39624	-0.32395
Pred. risk:acute PR	0.033	0.037	0.062	-0.089	0.155	-0.11055	0.03492	-0.17899	-0.04211

Table 3 Model output for the best-fitting Cox -model testing for an effect of NCE of lynx predation and human disturbance on non-lynx-related mortality risk. Model coefficients are reported together with the hazard ratios (exp(β)) and corresponding 95%-confidence intervals.

Variables	β	exp(β)	Lower CI	Upper CI
Log(Road distance)	-1.156	0.315	-1.877	-0.435
Chronic predation risk	1.558	4.75	0.731	2.386
Altitude	-0.628	0.533	-1.265	0.008

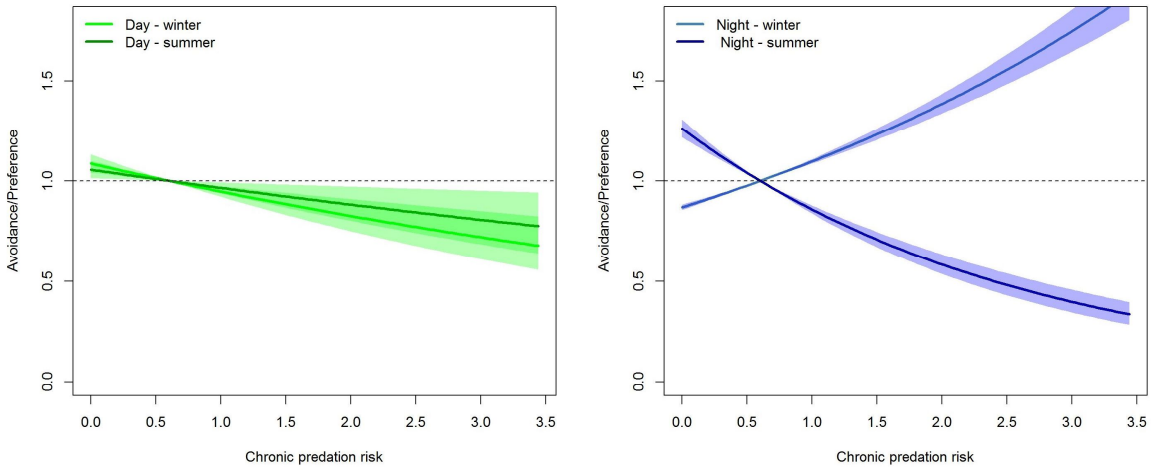

Figure 1 Selection coefficients of chronic predation risk during winter/summer for the day (green) and night (blue) model respectively. Selection curves together with the 95%-pointwise Confidence bands are shown. The dashed horizontal line at y=1 indicates no selection.

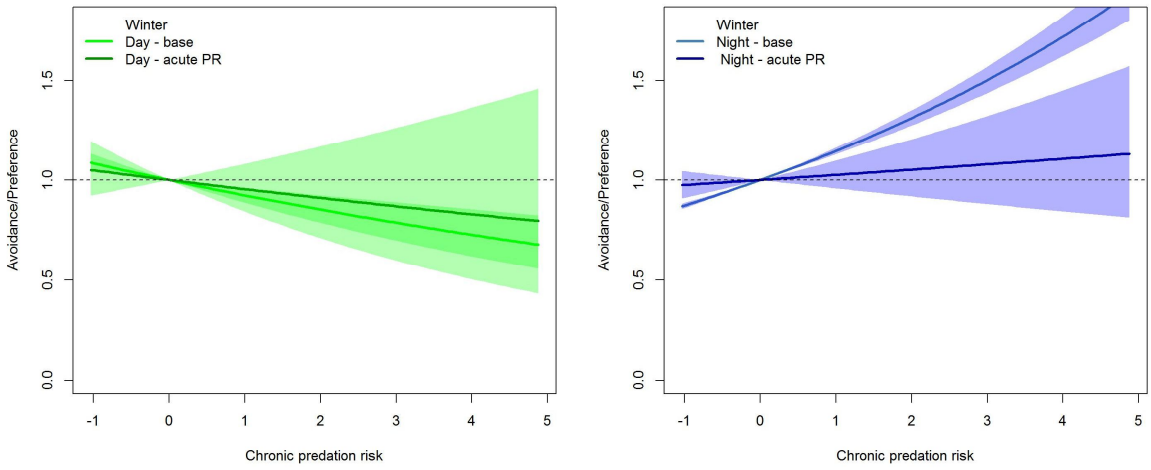

Figure 2 Selection of chronic predation risk in winter in the absence (base selection) of lynx compared to selection during acute predation risk (acute PR) when a lynx is present. Results from the day model are shown in green (left panel) and from the night model in blue (right panel). Selection curves together with the 95%-pointwise Confidence bands are shown. The dashed horizontal line at y=1 indicates no selection.

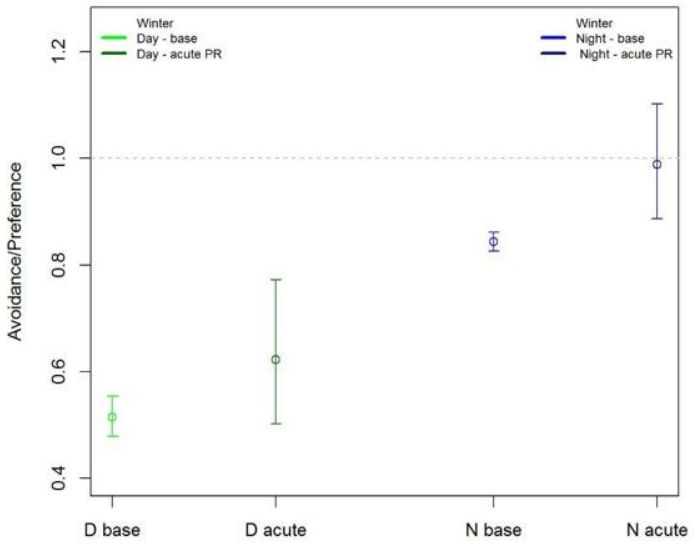

Figure 3 Selection of open habitat in winter in the absence (base) of a lynx compared to selection during acute predation risk (acute PR) when a lynx is present. Results from the day model are shown in green (left panel) and from the night model in blue (right panel). Point estimates together with the 95% confidence intervals are shown. The dashed horizontal line at y=1 indicates no selection.

Discussion

Behavioral responses to predator presence often come at a cost and there is a large body of literature suggesting that such non-consumptive effects (NCE) may be stronger than consumptive effects (CE; reviewed in Brown&Kotler 2004, Preisser et al. 2005, Peckarsky et al. 2008). Furthermore ecological theory predicts that ambush predators exert stronger NCE than active predators as they provide more persistent cues about predation risk than their widely roaming counterparts (Preisser et al. 2007, Schmitz 2008). In this study we quantified the NCE of the ambush predator, the European lynx, on one of its main prey, the European roe deer, and tested whether the predator-induced behavioral changes would have knock-on effects on deer survival. Furthermore we distinguished between chronic and acute predation risk according to the risky places and the risky times hypothesis and tested how these different risk components interact. Indeed we found that roe deer responded to both, chronic and acute predation risk very dynamically depending on the spatial and temporal context. These NCE were strong enough to affect non-lynx predation related mortality together with effects related to human disturbance.

In the following we discuss our findings in the light of the four predictions we made in the introduction:

1) Roe deer avoid areas of high chronic predation risk from lynx according to the risky places hypothesis.

Our findings show that roe deer respond to chronic lynx predation risk according to the risky places hypothesis. The observed patterns of chronic predation risk avoidance in this study can be explained in the light of varying environmental constraints to which roe deer are exposed in winter and summer or during day and night. During the day human activity is high whereas lynx activity is low. Due to this reason roe deer spend most of the daytime inside the forest away from humans but where the risk of being killed given a lynx encounter is higher than in the open (Lone et al. 2014). At night when lynx are active roe deer spend more time in the open where the risk of being killed given an encounter is lower. This pattern however is much weaker in winter, because roe deer are constrained by cold temperatures and dense snow cover which forces them to stay inside the forest even at night (Mysterud et al. 1999). Thus, in winter roe deer are forced to accept high levels of lynx predation risk at night due to severe weather conditions as has also been found in a study from Norway (Ratikainen et al. 2007). During summer nights on the other hand, roe deer strongly avoid chronic predation risk by lynx and spend most of the time in the open thereby reducing the risk of being killed by lynx. Thus by adjusting the antipredator response to the prevailing environmental constraints and risk situation roe deer manage to lower their exposure to chronic predation risk.

2) Roe deer avoid high chronic predation risk more during acute predation risk when a lynx is currently present according to the risky times hypothesis.

According to the risky times hypothesis, roe deer altered their antipredator behavior in situations of acute predation risk when a lynx was in their perceptual range. We found that roe deer increased their response to chronic predation risk during the night in situations of acute predate risk and thereby reduced the probability of encountering a lynx during the time when lynx are most active (Schmidt 1999). In contrast during the day the response of deer to chronic predation risk was the same irrespective of the immediate presence of a lynx. The reason for this may be, that during the day deer are more constrained by other factors such as avoiding humans and thus have to tradeoff between the different risk factors (Hewison et al. 2001). Moreover during the day lynx activity is low and therefore the probability of encountering a lynx is already reduced. These results confirm other studies that have found that prey respond to the immediate presence of predators and at the same time show the importance of incorporating the temporal dimension in predator-prey interactions (e.g. Valeix et al. 2009, Middleton et al. 2013, Latombe et al. 2014, Basille et al. 2015).

3) Roe deer will shift their habitat use to safer places and reduce their activity during acute predation risk according to the risky times hypothesis.

In addition to avoiding areas of higher encounter probabilities during acute predation risk, roe deer also shifted to safer habitats where the probability of being killed was lower. This was mainly achieved by moving into open habitat where it will be easier for a deer to detect an approaching lynx. A similar result has been found in a study of the effects of lions, also an ambush predator, on several ungulates species in an African savannah system (Valeix et al. 2009). On the other hand, our findings contrast with habitat shifts observed in prey species of wolves in North America. Wolves, being cursorial predators, are more successful when hunting in the open. Therefore prey species of wolves have been found to move away from open habitat when wolves were in close proximity (e.g. Latombe et al. 2014, Basille et al. 2015).

During the night roe deer also reduced their movement rates during acute predation risk, even though this effect was weak. Activity reduction under acute predation risk has been shown in different small rodent species and has been explained with reduced detection probability from predators (e.g. Kotler&Brown 1992, Borowski&Owadowska 2010). Activity reduction in roe deer in response to acute predation risk by lynx is likely to serve a similar purpose. Alternatively, reduced movement rates may simply be a consequence of not retreating into the risky forest for resting but rather stay in the open for both resting and feeding. Overall the results from prediction 2 and 3 together suggest that roe deer reduce the risk of being killed by a lynx by concurrently avoiding areas of high encounter probability (prediction 2) and at the same time move to safer habitat with increased predator detection probability (prediction 3).

4) Roe deer living in high predation risk areas suffer from increased non-lynx related mortality due to NCE.

The importance of NCE on prey population dynamics has been shown repeatedly in many different taxa (Preisser et al. 2005). Nonetheless, examples from large mammalian predator-prey systems are still rare (Creel et al. 2013). The results from our proportional hazard analysis (Table 1) suggest that deer living in areas of high chronic predation risk (risky places) suffer from increased non-lynx predation related mortality, indicative of strong NCE. This effect was even stronger than direct and indirect effects from human disturbance. Besides humans, lynx are the most important cause of mortality for roe deer where the two species co-occur and different studies have shown that lynx predation has an important impact on roe deer population dynamics (Nilsen et al. 2009, Melis et al. 2009). Thus far this impact has been mainly attributed to direct consumptive effects. The results of our study underline the importance of considering also NCE when assessing the overall impact of predators on their prey (Lima 1998). Furthermore our findings confirm predictions that ambush predators should exert strong NCE on their prey (Schmitz et al. 2005, Preisser et al. 2007). These findings together with results from other studies suggest that strong NCE that affect prey demography should be common also in large mammalian predator-prey systems.

Conclusions

There are only few studies on large mammals that quantified NCE and their knock on consequences on survival and reproduction of prey, most of which focused on the impact of wolves on elk in North America Creel et al. (2007, but also see Sheriff et al. 2009). Active predators such as wolves are predicted to have smaller NCE on their prey than ambush predators as their hunting mode should give less predictable cues that can be associated with certain habitat features than the hunting model from ambush predators (Preisser et al. 2007). However, recent studies have questioned the general applicability of these predictions to large mammalian predator-prey systems and even suggested the opposite (Creel et al. 2013, Creel et al. 2014). Indeed results from wolf-elk studies have been equivocal with some studies finding demographic knock on consequences from NCE whereas others did not (e.g. Creel et al. 2007, Middleton et al. 2013). Furthermore these studies have mainly looked at the effect of NCE on reproduction and did not look at the effects on survival (but see Christianson&Creel 2010). In our study, we show that a large mammalian ambush predator evoked strong NCE on one of its main prey by provoking shifts in habitat selection and activity reduction in response to variation in chronic and acute predation risk. Ultimately, these predator induced behavioral adaptations increased non-predation related mortality in the prey. We do not know whether the observed effects on survival

in roe deer are related to a reduction in foraging rate and quality, or due to a chronic stress response as a result of sustained 'psychological` stress (Clinchy et al. 2013). Comparisons of vigilance levels as well as diet composition and physiological state of deer over gradients of varying predation risk would be necessary to identify the ultimate causes of the observed reduction in survival. Moreover, we do not know at present if reduced survival really affects deer population growth. To test whether this is the case, it would be necessary to analyze to what extent reduced survival is compensatory or additive to other mortality causes. We encourage studies over multiple populations exposed to different levels of lynx predation and in different environmental contexts to shed more light on the processes determining the strength of NCE in this predator-prey system. Ultimately we need more research to understand how consumptive effects interact together with non-consumptive effects in shaping large mammalian predator-prey systems with contrasting predator types.

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References

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial Partitioning of Predation Risk in a Multiple Predator-Multiple Prey System. Journal of Wildlife Management 73:876-884.

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J.-P. Ouellet, and R. Courtois. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. Ecology 96:2622-2631.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour 76:611-618.

Borowski, Z., and E. Owadowska. 2010. Field vole (Microtus agrestis) seasonal spacing behavior: the effect of predation risk by mustelids. Naturwissenschaften 97:487-493.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999-1014.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399.

Burnham, K. B., and D. R. Anderson. 2002. Model Selection And Multimodel Inference: A Practical Information- Theoretic Approach. 2 edition. Springer-Verlag New York.

Christianson, D., and S. Creel. 2010. A nutritionally mediated risk effect of wolves on elk. Ecology 91:1184-1191.

Clinchy, M., M. J. Sheriff, and L. Y. Zanette. 2013. Predator-induced stress and the ecology of fear. Functional Ecology 27:56-65.

Coulon, A., N. Morellet, M. Goulard, B. Cargnelutti, J.-M. Angibault, and A. J. M. Hewison. 2008. Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. Landscape Ecology 23:603-614.

Creel, S., D. Christianson, S. Liley, and J. A. Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960-960.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773-784.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Creel, S., and J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour 69:1181-1189.

Creel, S., J. A. Winnie, D. Christianson, and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. Animal Behaviour 76:1139-1146.

Creel, S., J. A. Winnie, Jr., and D. Christianson. 2013. Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: an example with wolves and elk. Ecology and Evolution 3:5189-5200.

Danilkin, A., and A. J. M. Hewison. 1996. Chapman and Hall Wildlife Ecology and Behaviour Series: Behavioural ecology of Siberian and European roe deer. Chapman and Hall Wildlife Ecology and Behaviour Series; Behavioural ecology of Siberian and European roe deer:xvi+277p-xvi+277p.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society B: Biological Sciences 365:2233-2244.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554-3565.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.

Fortin, D., M.-E. Fortin, H. L. Beyer, T. Duchesne, S. Courant, and K. Dancose. 2009. Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. Ecology 90:2480-2490.

Gehr, B., Hofer, E.J., Muff, S., Ryser, A., Vimercati, E., Vogt, K., Keller, L.F. Spatial scale and behavioral state interact in shaping temporal dynamics of habitat selection in Eurasian lynx (In review).

Gehr, B., Hofer, E.J., Ryser, A., Vimercati, E., Vogt, K., Keller, L.F. Caught in the crossfire of two predators – Hunting mediated predator facilitation results in superadditive mortality of European roe deer by Eurasian lynx (In prep).

Hebblewhite, M., E. Merrill, and T. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos 111:101-111.

Hewison, A. J., J. P. Vincent, J. Joachim, J. M. Angibault, B. Cargnelutti, and C. Cibien. 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. Canadian Journal of Zoology 79:679-689.

Kotler, B. P., L. Blaustein, and J. S. Brown. 1992. Predator Facilitation - The Combined Effect Of Snakes And Owls On The Foraging Behavior Of Gerbils. Annales Zoologici Fennici 29:199-206.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors Affecting Gerbil Foraging Behavior And Rates Of Owl Predation. Ecology 72:2249-2260.

Latombe, G., D. Fortin, and L. Parrott. 2014. Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. Journal of Animal Ecology 83:185-198.

Lone, K., L. E. Loe, T. Gobakken, J. D. C. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos 123:641-651.

Melis, C., B. Jedrzejewska, M. Apollonio, K. A. Barton, W. Jedrzejewski, J. D. C. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K. Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka, and S. Zhyla. 2009. Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Global Ecology and Biogeography 18:724-734.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023-1030.

Mysterud, A., L. B. Lian, and D. O. Hjermann. 1999. Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1486-1493.

Nilsen, E. B., J. M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. van Laere, and J. D. C. Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. Journal of Animal Ecology 78:585-594.

Padie, S., N. Morellet, A. J. M. Hewison, J.-L. Martin, N. Bonnot, B. Cargnelutti, and S. Chamaille-Jammes. 2015. Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos 124:1536-1546.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416-2425.

Pellerin, M., C. Calenge, S. Said, J. M. Gaillard, H. Fritz, P. Duncan, and G. Van Laere. 2010. Habitat use by female western roe deer (Capreolus capreolus): influence of resource availability on habitat selection in two contrasting years. Canadian Journal of Zoology-Revue Canadienne De Zoologie 88.

Periquet, S., L. Todd-Jones, M. Valeix, B. Stapelkamp, N. Elliot, M. Wijers, O. Pays, D. Fortin, H. Madzikanda, H. Fritz, D. W. Macdonald, and A. J. Loveridge. 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. Behavioral Ecology 23:970-976.

Pesenti, E., and F. Zimmermann. 2013. Density estimations of the Eurasian lynx (Lynx lynx) in the Swiss Alps. Journal of Mammalogy 94:73-81.

Plank, M. 2013. Habitat modelling of alpine ibex - Capra ibex - in the Swiss National Park and the National Park Hohe Tauern - A comparison. Universität für Bodenkultur, Wien.

Preisser, E., J. Orrock, and O. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. Ecology 88:2744-2751.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ratikainen, I. I., M. Panzacchi, A. Mysterud, J. Odden, J. Linnell, and R. Andersen. 2007. Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. Journal of Zoology 273:192-199.

Schmidt, K. 1999. Variation in daily activity of the free-living Eurasian lynx (Lynx lynx) in Bialowieza Primeval Forest, Poland. Journal of Zoology 249:417-425.

Schmitz, O. 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319:952-954.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78:1249-1258.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology 92:398-407.

Therneau, T. M., and P. M. Grambsch. 2000. Modeling Survival Data: Extending the Cox Model. 1 edition. Springer-Verlag New York.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement ecology 2:4-4.

Valeix, M., A. J. Loveridge, S. Chamaille-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. Ecology 90:23-30.

van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84:723-735.

Visscher, D. R. 2006. GPS measurement error and resource selection functions in a fragmented landscape. Ecography 29:458-464.

Weissburg, M., D. L. Smee, and M. C. Ferner. 2014. The Sensory Ecology of Nonconsumptive Predator Effects. American Naturalist 184:141-157.

White, P. J., R. A. Garrott, K. L. Hamlin, R. C. Cook, J. G. Cook, and J. A. Cunningham. 2011. Body condition and pregnancy in northern Yellowstone elk: Evidence for predation risk effects? Ecological Applications 21:3-8.

Zimmermann, F., and U. Breitenmoser. 2002. A distribution model for the Eurasian lynx (Lynx lynx) in the Jura Mountains, Switzerland. Predicting Species Occurrences: Issues of Accuracy and Scale:653-659.

Zimmermann, F., D. Foresti, J. Bach, N. Dulex, C. Wuersten-Breitenmoser, and U. Breitenmoser. 2014. Abundanz und Dichte des Luchses in den Nordwestalpen: Fang-Wiederfang-Schätzung mittels Fotofallen im K-VI im Winter 2013/14.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Mixed Effects Models and Extensions in Ecology with R.

Supporting Information Appendix S1

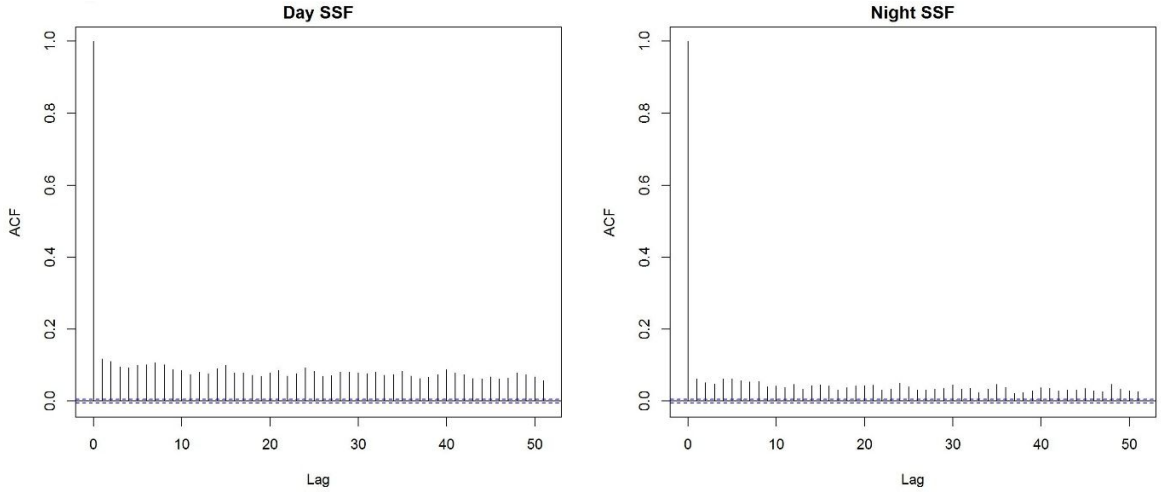

Figure S1 Autocorrelations of the deviance residuals of the day (left panel) and night model (right panel) respectively. We considered autocorrelations to be negligible below values of 0.1. According to this criteria autocorrelation became negligible for deer steps during the day after 24 steps (48 hours) whereas at night there was no autocorrelation present in the deviance residuals.

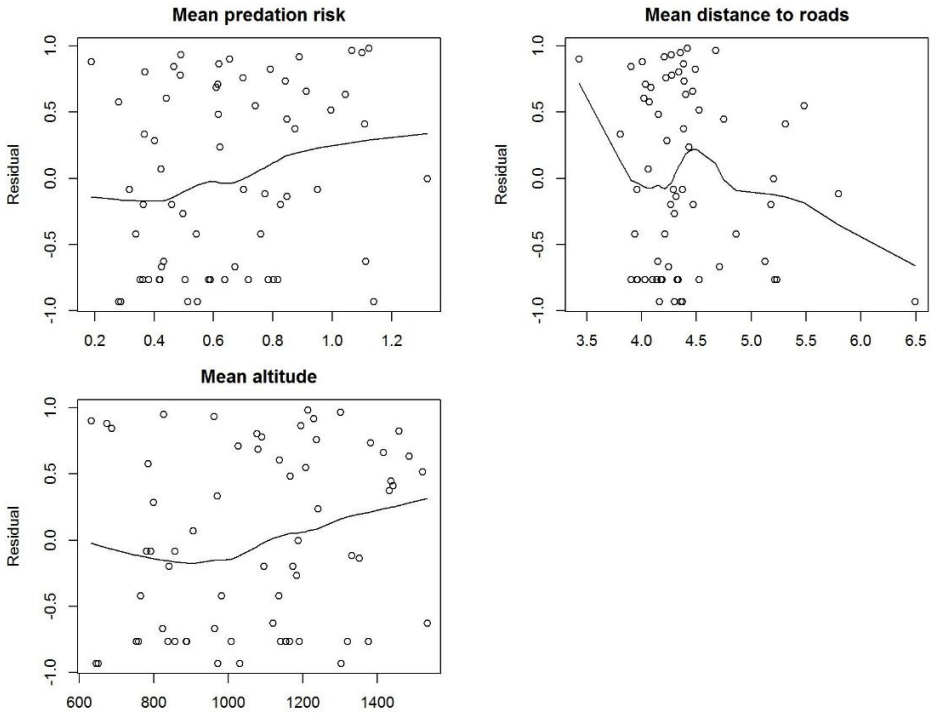

Figure S2 The functional form of the relationship between the predictor variables and the hazard function for the best Cox-model. The martingale residuals of the null model (β=0) are plotted against each of the three predictors separately together with a superimposed scatterplot smooth.

General Discussion

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Humans can be considered as ecological players of ecosystem processes that shape the behavior and demography of their commensal species. In the presence of humans large top predators may be downgraded in the food chain or compete with humans for their prey (Oriol-Cotteril et al. 2015). Furthermore prey species themselves have to tradeoff between risk avoidance towards humans or their natural predators (e.g. Nilsen et al. 2009). Only few studies have considered the implications of this tradeoff for the behavioral response game between large predators and their prey and how space use patterns and habitat selection are affected when a new player enters the game (Orio-Cotteril et al. 2015). In this thesis I have addressed these questions for the predator-prey system of lynx and roe deer in the North-Western Alps of Switzerland. In the first chapter I focused on tradeoffs in lynx habitat selection between anthropogenic risks and prey density and found that lynx used areas of high prey density during times of low human activity. Furthermore habitat selection was influenced by the behavioral state and the spatial scale considered. In the second chapter I focused on the prey and tested how lynx and humans interact in shaping space use patterns of roe deer during the hunting season in fall. The results of this second chapter show that hunters facilitated lynx predation which resulted in superadditive mortality for deer during the hunting season. Finally in the third chapter I looked at non-cosumptive effects (NCE) in roe deer in response to lynx predation risk and found that the strong behavioral response to high lynx predation risk increased non-lynx-related mortality of roe deer in the study area.

The results from habitat selection models of lynx in the first chapter reveal the high plasticity of large predators when it comes to adapting to new situations of risk and prey distribution. Moreover the findings show how important it is to take the temporal dimension into account when modelling animal habitat selection in general. In an environment that is so heavily affected and altered by humans such as most of Europe (except for some parts of Noth-Eastern Europe) there is not much room for a spatial separation between large predators and humans (Chapron et al. 2014). Thus the utilization of temporal refuges, for instance by shifting their activity to night hours offers the opportunity to these elusive species to persist even in areas of high population density. Such temporal shifts in activity in response to human disturbance as observed in this study for the lynx, have also been reported for other large predators such as bears and wolves (Ordiz et al. 2012, Zimmermann et al. 2014). However, we need to better understand what intrinsic (e.g. behavioral state) and extrinsic (e.g. habitat edges) factors shape large predator space use patterns and habitat selection in order to identify the basic habitat requirements that need to be fulfilled in order to sustain viable populations in close proximity to humans. In a highly structured landscape these requirements will also depend on the spatial scale considered. In the case of lynx for instance the existence of good prey habitat at southern exposed slopes in mountainous areas may be a criteria for a high quality lynx habitat at the home range scale whereas at the patch scale habitat selection will depend more on the specific behavioral state of the animal and the existence of refuge time periods during which human disturbance is low. Such

knowledge about habitat requirements at different spatial scales will help to elaborate efficient conservation measures and to keep human-wildlife conflicts at a minimum. The recovery of all three large predators in Europe, namely bears (Ursus arctos), wolves (Canis lupus) and lynx exemplify the great adaptive potential of these species and provide hope for the conservation of large carnivores in other parts of the world where growing human populations are intensifying human-wildlife conflicts with large carnivores (Linnell et al. 2005, Ripple et al. 2014). Thus the conservation of large top carnivores in human-dominated landscapes will enable us to maintain and reestablish functioning ecosystems in Europe and other parts of the world in the light of a growing human population in the future.

In chapter 2 I could show the importance of considering humans as an ecological player in predator-prey dynamics. The results indicate that humans can alter the natural risk landscape of a prey, and induce behavioral changes that can result in super-additive mortality through predator facilitation. In this context it is important to consider that the interaction between humans and large predators could be both positive (i.e. facilitation) or negative (i.e. competition or intraguild predation; Sih et al. 1998). Furthermore, depending on the direction of the interaction (positive or negative), implications for prey and also lower trophic levels will be different. In a study in California, cougar females reduced the consumption time and increased their kill rate on mule deer in areas of high human disturbance (Smith et al. 2015). This premature abandonment of kills could negatively affect predator and prey populations alike through increased energetic costs for hunting in cougars or increased mortality in mule deer prey (a mechanism that could also play a role for lynx and roe deer and requires further research). However, in the case of humans killing large predators or competing with them for prey, the effect for the prey population could be positive, even if humans themselves hunt the prey as in the case for roe deer in this study (Côté et al. 2004). The killing of predators by humans is a form of intraguild predation and may result in an overall risk reduction for the prey and therefore affect the latter positively (Sih et al. 1998). The same would be true if hunting induced behavioral changes in a game species that reduces the success rate of both hunters and predator. The behavior of the prey is therefore very important for understanding the ecological role of humans in predator-prey dynamics and needs to be considered in studies on predator-prey interactions.

The number of possible interactions increases with the number of players in a functioning Ecosystem. Thus in more complex communities it is very difficult to foresee the possible effect that adding an additional top predator (e.g. humans) may have to the dynamics of a system. Humans and large predators have large potential impact on top-down processes and direct and indirect interactions with lower trophic levels can change ecosystem dynamics and result in trophic cascades (Carpenter et al. 1987, Werner&Peacor 2003, Schmitz et al. 2004). We are far from understanding how humans affect predator-prey systems. Nonetheless, considering the ecological role of humans in human-dominated landscapes is very important to understand the

dynamics of such ecosystems and is key for the development of efficient wildlife management plans that are needed for the conservation of large predators and their prey alike.

The results from the last chapter of this thesis provide evidence that lynx predation evokes strong NCE in roe deer and are in accordance with the prediction that ambush predators should exert pronounced behavioral responses in their prey that can have knock-on consequences on prey survival or reproduction . Most evidence for the aforementioned hypothesis comes from studies on invertebrates or small vertebrate systems (Preisser et al. 2007). However, results from large mammalian predator-prey systems in the past have been equivocal (Thaker et al. 2011, Middleton et al. 2013, Creel et al. 2014). Creel et al. (2013) even suggested that for large mammalian predator-prey systems, such as wolves and elk in Yellowstone, the relationship may be reversed. An opinion the authors reinforce in a different study on a multiple predator-prey system in a savannah ecosystem in Africa (Creel et al. 2014). Even though the present study is an example of strong NCE of an ambush predator on one of its main prey with convincing evidence for knock-on effects on prey survival, one should not dismiss that other factors than the predators hunting mode may be important in predicting the strength of NCE. Schmitz et al. (2004) suggested that predator hunting mode in combination with the habitat domain of predator and prey are the key drivers of NCE strength. Even though Preisser et al. (2007) only found weak support for the importance of habitat domain on NCE in a meta-analysis on predator-prey interactions, the authors mention that this issue requires further testing. The authors could not exclude some sampling bias in their meta-analysis and further discussed the complicating influence of multiple predators for one prey (i.e. more than one predator feeding on the same prey). Indeed I found in this study that humans (an additional predator of roe deer besides lynx) also affected deer survival. Thus in future studies on the strength of NCE in large vertebrate predator-prey systems one should also consider the habitat domain of predators and prey and account for the impact of humans or other predators. It seems likely that the degree of overlap/non-overlap in habitat domain of predator and prey will have an important impact on the outcome of the behavioral response game of hide and seek between the two players (Schmitz et al. 2004). In addition the presence of other predators (including humans) of the same or different hunting mode may result in risk reduction or risk enhancement which in turn may affect the strength of NCE (Sih et al. 2005). The findings of this study together with results from other studies suggest that strong NCE affecting prey demography should be common also in large mammal species. But more research is required to understand the complex interplay between predator hunting mode, predator and prey habitat domain and multiple predators in order to be able to predict the strength and direction of these interactions.

Concluding remarks

In this thesis I focused on identifying key drivers involved in shaping space use patterns of a large ambush predator and one of its main prey. Furthermore I characterized the spatiotemporal drivers of habitat selection and risk avoidance of both players in a human-dominated environment. The presented results show the tradeoffs between risk avoidance and food acquisition that affect decision making of all animals. Furthermore, the findings highlight the role of humans as ecological drivers of Ecosystem processes. Humans can be considered as top predators that compete with other predators for prey, but are also responsible for intraguild predation or predator facilitation. This creates a complex landscape of fear that shapes habitat selection of wildlife living in human-dominated environments. However, the presented results also show that animals are able to adapt to those challenges by using spatiotemporal refuges that enable the coexistence of humans and wildlife in areas as densely populated as Central Europe.

Finally I presented possible directions for future research in order to investigate the different factors involved in predicting the effect of human activities on wildlife interactions and to better understand the role of predator hunting mode and habitat domain on shaping large mammalian predator-prey dynamics.

References

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. Vonende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68:1863-1876.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andren, J. Vicente Lopez-Bao, M. Adamec, F. Alvares, O. Anders, L. Balciauskas, V. Balys, P. Bedo, F. Bego, J. Carlos Blanco, U. Breitenmoser, H. Broseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjaeger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremic, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majic, P. Maennil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Myslajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunovic, J. Persson, H. Potocnik, P.-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinsek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajce, E. Tsingarska-Sedefcheva, M. Vana, R. Veeroja, P. Wabakken, M. Woefl, S. Woelfl, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517-1519.

Cote, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology Evolution and Systematics 35:113-147.

Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773-784.

Creel, S., J. A. Winnie, Jr., and D. Christianson. 2013. Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: an example with wolves and elk. Ecology and Evolution 3:5189-5200.

Linnell, J. D. C., C. Promberger, L. Boitani, J. E. Swenson, U. Breitenmoser, and R. Anderson. 2005. The linkage between conservation strategies for large carnivores and biodiversity: the view from the "half-full" forests of Europe. Large carnivores and the conservation of biodiversity.:381-399.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023-1030.

Nilsen, E. B., J. M. Gaillard, R. Andersen, J. Odden, D. Delorme, G. van Laere, and J. D. C. Linnell. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. Journal of Animal Ecology 78:585-594.

Ordiz, A., O.-G. Stoen, S. Saebo, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation 152:21-28.

Oriol-Cotteril, A., M. Valeix, L. G. Frank, C. Riginos, and D. W. McDonald. 2015. Landscapes of coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124:10.

Preisser, E., J. Orrock, and O. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. Ecology 88:2744-2751.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343:151-+.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153-163.

Sih, A. 2005. Predator-Prey Space Use as an Emergent Outcome.in P. Barbosa and I. Castellanos, editors. Ecology of Predator-Prey Interactions. Oxford University Press.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350-355.

Smith, J. A., Y. Wang, and C. C. Wilmers. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. Proceedings of the Royal Society B-Biological Sciences 282.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology 92:398-407.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.

Zimmermann, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behavioral Ecology 25:1353-1364.

Author contributions

Chapter 1

Benedikt Gehr conducted the analysis and wrote the manuscript. Lukas Keller and Stefanie Muff provided advice and reviewed the manuscript. Kristina Vogt provided advice, reviewed the manuscript and collected data in the field. Elizabeth Hofer, Andreas Ryser and Eric Vimercati collected the Data in the field.

Chapter 2

Benedikt Gehr collected the roe deer data, conducted the analysis and wrote the manuscript. Lukas Keller provided advice and reviewed the manuscript. Kristina Vogt provided advice and collected the Lynx data in the field. Elizabeth Hofer, Andreas Ryser and Eric Vimercati collected the Lynx-data in the field.

Chapter 3

Benedikt Gehr collected the roe deer data, conducted the analysis and wrote the manuscript. Lukas Keller provided advice and reviewed the manuscript. Elizabeth Hofer, Andreas Ryser, Eric Vimercati and Kristina Vogt collected the Lynx-data in the field.

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